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# JOURNAL OF MORPHOLOGY.

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## THE ACTINIARIA OF THE BAHAMA ISLANDS, W.I.

J. PLAYFAIR McMURRICH, M.A., PH.D.

DURING the summer of 1887 the Marine Zoölogical Station of the Johns Hopkins University was established near Nassau, the capital of the Bahama Islands, W.I., situated upon the island of New Providence. Through the courtesy of the Director of the Station, Dr. W. K. Brooks, I was able to make use of the facilities offered by the Station, and a portion of my stay of five weeks was occupied in studying the Actinian fauna of the neighborhood. For the most part, my observations were confined to the vicinity of the Station; but a few excursions were made to neighboring islands, and on one occasion I visited a cove situated a couple of miles to the westward of Nassau.

In 1886 the Johns Hopkins Station was located on Green Turtle Cay, upon the eastern side of Great Abaco Island, one of the islands of the Little Bahama Bank, lying some hundred miles to the north of New Providence. While there, the artist, Mr. Uhthoff, who accompanied the expedition of that year, made colored sketches in oils of the commoner Actinia collected. These drawings Dr. Brooks kindly handed over to me, and though wanting sufficient attention to details, nevertheless allow of ready identification by one acquainted with the living specimens. The chief value of the drawings lies in their demonstration of the similarity of the forms inhabiting the Little Bahama Bank to those found farther south, all the species represented, with one exception, having been found at New Providence.

All the forms collected were littoral in their habitat. Owing to the want of the proper facilities I was unable to do any dredging in deep water.

A few remarks upon the methods of preserving Actiniæ are necessary. The object of my visit to New Providence being partly to obtain material for class work and specimens for use in the illustration of my lectures, I was unable to devote as much time as could be wished to the study of the living specimens of Actiniæ. All that I was able to do was to make careful colored sketches of the various forms collected. The preservation of Actiniæ in a suitable condition for future study is a matter of some difficulty, and has greatly hindered a thorough study of the group. The great difficulty experienced in killing the animals sufficiently rapidly to prevent contraction is the main obstacle, and the method of first producing torpor by the use of chloroform or nicotine, as practised by the Hertwigs ('79), is tedious and not always successful. I was in hopes that good results might be obtained by the use of cocaine, but my experiments with it gave negative results. The success of any method depends greatly on the character of the form under treatment. Methods which will give good results with the Zoanthidæ, for instance, will yield failure quite as often as success with more contractile forms. For a collector who cannot give the time required for the proper carrying on of the narcotizing methods, my experience has led me to advise the following method of procedure. After the general characteristics—the coloration, presence or absence of tubercles, the dimensions, and such easily observable features—have been carefully noted with as much detail as possible, the animal is placed in a jar just wide enough to allow its complete expansion, and with just enough water to cover it when fully expanded. When this condition is reached, a glass syringe is filled with Perenyi's fluid, and this is suddenly and rapidly injected into the interior of the animal, the nozzle of the syringe having been quickly inserted into its mouth. At the same time, if possible, a quantity of the same fluid is poured over the animal, so that it is bathed without and within with a tolerably strong mixture of Perenyi's fluid. It is left to the action of the fluid for about half an hour, and is then to be treated successively with 50, 70, and 90 per cent alcohol, care being taken to inject a considerable quantity of the spirits into the interior at each change.



Although considerable contraction usually results from this process, and although the color is, as a rule, almost destroyed, yet I think the distortion is less than that resulting from most other methods, and there is the great advantage that the parts are preserved in a satisfactory manner for future histological study. Dissection is possible, owing to the absence of the excessive brittleness which results from the use of chromic acid, encrusting or attached calcareous particles are dissolved, and sectioning of entire small forms may be practised without the danger of ruining the knife, and, lastly, there is no unpleasant precipitation of crystals as occurs from the use of corrosive sublimate when the subsequent washing has not been sufficiently prolonged.

So far as I am aware, there exist no records of observations upon the Actinaria of the Bahamas, although quite a number of forms have been described from others of the West Indian islands. Duchassaing and Michelotti ('60 and '66) have described many of the forms occurring in the Antilles; but in their observations they took account only of external characteristics, and even with regard to these their descriptions are often so imperfect as to render it difficult to ascertain the true relationships of the forms under consideration. Lesueur ('17) has also described several forms from the Antilles; and, lastly, Ellis has mentioned and figured one or two specimens in a letter to the Earl of Hillsborough published in the *Philosophical Transactions* ('67).

Owing to the great confusion which exists in the synonymy and classification of the Actinaria, notwithstanding Andres' excellent work ('83), it will be necessary to map out the exact limitations of the various groups and forms to be described here; and in most cases an historical review of the synonymy will be required.

Before concluding these introductory remarks I must acknowledge the obligation under which I rest to the officers of the Academy of Natural Sciences of Philadelphia, through whose courtesy and kindness I was permitted to make use of the magnificent library of that institution. Without this favor I should have been unable to unravel many of the tangled threads of synonymy which the investigations to be discussed in the following pages brought to my notice.

## ACTINIARIA.

## Tribe HEXACTININÆ, Hertwig.

Actiniaria, with paired mesenteries, those of each pair provided with longitudinal muscle fibres on the faces turned towards each other, and transverse fibres on the faces turned away from each other, — except in the case of two pairs, the directives, in which the arrangement is reversed, the longitudinal muscle fibres being upon the outer surfaces, and the transverse fibres on the inner. The number of the pairs of mesenteries present is at least six, and they increase in multiples of six.

## Sub-tribe ACTININÆ

= Family Actininæ, Andres.

Hexactininæ, with simple uniform tentacles, situated towards the periphery of the disc, so as to leave the central portion bare; each tentacle corresponds to an intraseptal space, and they are arranged in cycles, and not in radial series.

## Family Sagartidæ, Hert.

Actininæ, adhering to foreign bodies by a flat, contractile base. Column smooth, or provided with verrucæ or tubercles, and perforated by cinclides. Sphincter muscle usually well developed and imbedded in the mesogloea,<sup>1</sup> occasionally absent or very feebly developed (Aiptasia). The mesenteries of the first cycle alone are perfect, and are not gonophoric, the reproductive organs being borne by the mesenteries of the second and third cycles. The free edges of all the septa with mesenterial filaments bear acontia. The tentacles are smooth, cylindrical, entacmæous, and are arranged in regular cycles.

The definition of the family Sagartidæ given above is essentially identical with that of R. Hertwig ('82), the only difference

<sup>1</sup> Being convinced that the supporting layer of the Actiniaria cannot be considered homologous with the mesoderm of the higher forms, I have adopted for its designation the term mesogloea proposed by Bourne (*Quart. Journ. Micr. Sci.*, N.S., Vol. XXVII., 1887).



being that I exclude the genus *Bunodes* which Hertwig includes in it, on the ground that since one of the forms originally included in that genus by Gosse — *B. coronata* — possesses acontia, there is a possibility that all the members of the genus may possess them, though as yet they have not been observed. The truth of the matter is that the so-called *Bunodes* with acontia described by Gosse ('60) and Hertwig really are Sagartidæ, the former belonging, as Andres has pointed out, to the genus *Chitonactis* of Fischer ('75), while the latter is a *Cylista*. The external character, the possession of warts arranged in parallel rows, is of small importance compared with the internal structural characters, which in the true Bunodidæ are very different from what is to be found in the Sagartidæ. In his later paper ('88), Hertwig corrects the mistake he made in considering his *Cylista minuta* a *Bunodes*.

Gosse's family, Sagartidæ, is slightly different in the forms included, the difference being due partly to ignorance regarding the structure of non-British forms, and partly to the attributing of too much importance to external characters. *Discosoma*, which he assigns to this family, belongs really to an entirely different sub-tribe, and *Aiptasia*, which he places among the Antheadæ, ought to be included. The sub-family Sagartinæ of Verrill ('68) and Klunzinger ('77), and the Sagartidæ of Andres ('83), differ from the group as I have defined it above by the exclusion of *Phellia* and allied genera on account of their possession of an external investment. It seems hardly correct, however, to make of the *Phellia* forms a group equivalent to the Bunodidæ, for instance; I should prefer an arrangement of this kind, —

Family Sagartidæ.

(The definition as above.)

Sub-family Sagartinæ.

Sagartidæ, without any external membranous investment.

Sub-family Phellinæ.

Sagartidæ, with an external membranous investment.

## Genus AIPTASIA, Gosse.

*Synon.* — *Actinia* (pars) — Auct.

*Cribrina* (pars) — Schmarda.

*Dysactis* (pars) — Milne-Edwards, 1857.

*Aiptasia* — Gosse, 1860.

*Paranthea* — Verrill, 1866.

*Bartholomea* — Duchassaing and Michelotti, 1866.

*Sagartia* (pars) — Jourdan, 1880.

*Sagartidæ*, with cinclides arranged in from one to several horizontal rows around the middle of the column. No verrucæ. Sphincter muscle either absent or very feebly developed.<sup>1</sup> Tentacles strongly entacmæous.

This genus was established by Gosse for *A. Couchii*, and includes forms which have been variously assigned to the genera *Sagartia*, *Actinia*, *Anthea*, etc. In fact, not a little confusion exists with regard to the genus. Milne-Edwards ('57) established the genus *Dysactis*, which he referred to his section of "Actinines vulgaires," forms with a smooth surface, and unperforated walls, the distinguishing characteristics of the genus being the absence of verrucæ and of "tubercules calicinaux," and the possession of entacmæous tentacles arranged in two cycles. The absence of cinclides and acontia would incline one to deny any similarity between this genus and Gosse's *Aiptasia*, but, since two at least of the four original species of *Dysactis* are now known to possess these structures, we must consider the imperfect knowledge of the forms the cause of the erroneous association of species found in the genus. It is to be noticed in this connection that the form which Verrill in his earliest paper ('64) refers to the genus *Dysactis* is, as I have satisfied myself by the examination of specimens, really an *Aiptasia* — *A. pallida*. Subsequently ('66), Verrill made this form the type of a new genus *Paranthea*.

The genus *Dysactis* must be considered synonymous in part with Gosse's *Aiptasia*, but on account of the imperfection of the definition, it seems preferable to disregard its priority and to retain the latter name. As stated above, Gosse ('60), though recognizing the presence of cinclides and acontia, separated his

<sup>1</sup> In neither of the species described here is there any trace of a circular muscle, and the same is the case with *A. diaphana*, according to the Hertwigs ('79). I have found, however, in *A. pallida* a slightly developed muscle imbedded in the mesoglossæa.



genus from the family Sagartidæ to which it properly belongs, and, making the inability to retract the tentacles of too great importance, placed it with the Anthedæ.

Duchassaing and Michelotti ('66), apparently overlooking Gosse's *Aiptasia*, established a new genus *Bartholomea*, whose definition differs from the original description of *Aiptasia* only in that the position of the cinclides towards the equator of the column is particularly mentioned, the genus being thus separated from *Adamsia* on the one hand, and *Nemactis* on the other. Milne-Edwards' genus *Dysactis* is also retained by these authors, the form referred to it being probably an *Aiptasia* whose cinclides were not very distinct.

1. *Aiptasia annulata* (Les.), And. (Pl. I., Fig. 1; Pl. III., Fig. 1.)

*Synon.* — *Actinia annulata*, n.s. — Lesueur, 1817.

*Dysactis annulata* — Milne-Edwards, 1857.

*Aiptasia annulata* — Andres, 1883.

*Actinia solifera*, n.s. — Lesueur, 1817.

*Paractis solifera* (*Actinia*) — Duchassaing and Michelotti, 1860.

*Bartholomea solifera* — Duchassaing and Michelotti, 1866.

*Aiptasia solifera* — Andres, 1883.

My reasons for uniting the two genera described by Lesueur ('17) will be more suitably discussed after the form which I studied has been described.

My specimens were found attached to the lower surface of the blocks of coral rock, or in cavities in these, along the shore of New Providence. Among the forms figured by Mr. Uhtoff I notice one which is evidently *A. annulata*, and Lesueur's specimen was obtained in the hollows formed in the madreporic rocks upon the shores of the island of Barbadoes. The form known as *A. solifera* was found by Lesueur and Duchassaing and Michelotti at Guadaloupe and St. Thomas, according to Lesueur, in old shells, particularly those of *Turbo versicolor* (?). This species consequently ranges from the Little Bahama Bank as far south, at any rate, as Barbadoes.

The coloration of all my forms was constant (Pl. I. Fig. 1). The column is for the most part pure white, shading off above into a pale brown, being in this darker region flecked with opaque white. The cinclidal tubercles are usually more transparent than the surrounding surface, and therefore are quite evident. The disc is brown, with white triangular spots at the

bases of the tentacles of the two inner cycles, towards which irregular white markings radiate from the white peristome. The tentacles are brown, ringed with connivent white bands.

The base is adherent and slightly larger than the column, and is sufficiently thin to allow the attachment of the mesenteries to shine through, giving rise to an appearance of white lines radiating from the centre to the periphery. In preserved specimens the base is always larger than the column, there being usually a strong constriction immediately above it. The limbus is usually more or less crenate.

The column is cylindrical and exceedingly extensible. When fully extended it measures about 3.6 cm. (according to Lesueur 5-7.5 cm.), with a diameter of 1.8 cm. About midway between the limbus and the margin it is provided with a series of cinclides. Occasionally these are situated somewhat above the middle, and occasionally slightly below it, but never so low as to resemble the genus *Adamsia*. The arrangement of the cinclides, which open on tubercles very evident in preserved specimens, is somewhat irregular. They are arranged in vertical series situated at regular intervals, but the number in each series varies. Occasionally each series consists of a pair, only one being placed immediately below the other, or the lower one may be slightly to the side, so as to appear almost as if alternate. Quite frequently three cinclides are to be found in each series, and in one form I counted as many as twelve in some of the series, the number in all of them being over three. This irregularity is prevalent throughout all the forms I have examined, and a definite statement as to the number of horizontal rows in which the tubercles are arranged is impossible, since not only does the number in the various vertical series vary in different specimens, but even in the same individual while there may be six tubercles in one series, in the next there may be only one, and so on.

The acontia are not emitted with as much readiness as in some other species of *Aiptasia*, and it is probably on this account that Lesueur failed to perceive and record their presence. I have seen them as white filaments protruded in considerable numbers through the cinclides.

In none of the specimens that I examined were any signs of a sphincter muscle observed. It is noteworthy that in one



specimen there was apparently a total absence of "yellow-cells" in the endodermal epithelium, while in others they were abundantly present.

The tentacles are decidedly entacmæous and very long, the inner ones measuring 3.4 cm. in length. In all the specimens examined they were arranged octamerously in five cycles, the formula being 8, 8, 16, 32, 64. Lesueur states that the "centre tentacula are about 6 or 8 in number," and gives their length as somewhat greater than those I measured; *i.e.*, two or three inches. Whether the words quoted mean that the numbers given were simply approximate, or that in some forms the arrangement of the tentacles was hexamerous and in others octamerous, it is impossible to say; in no case have I observed the hexamerous arrangement. One of the most striking peculiarities of the species is the occurrence upon the tentacles of a number of elevated bands, one above the other, each extending only partly round the tentacle, the successive bands being connivent. They are usually of a different color from the rest of the tentacle, and in preserved specimens stand out very prominently. In transverse sections they are seen to be due to thickening of the ectoderm, the mesogloea not participating in their formation. In the thickening are numbers of nematocysts, while elsewhere these are few in number and apparently smaller, or else absent. The ectodermal muscular layer of the tentacles is not markedly developed, presenting no foldings in fully extended tentacles, and no traces of muscle cells enclosed in the mesogloea. On account of the absence of a circular muscle the tentacles are not infolded during contraction.

The septa of the forms examined were in four cycles, the formula being 8, 8, 16, 32, and only those of the first cycle were perfect. A large mesenterial stoma is plainly visible on a level with the cinclides,—the outer one,—while the inner one is considerably smaller, but still quite evident. The Hertwigs ('79) state that in *A. diaphana* the inner stoma is the only one present, a statement which needs revision. There can be no question as to the existence of both the inner and the outer stoma in *A. annulata*, the size of the latter rendering all doubts as to its existence impossible.

The longitudinal muscle bands are well developed, and in the primary mesenteries (Pl. III., Fig. 1) occupy about  $\frac{4}{7}$  of the

width of the mesentery. Towards the point of its insertion into the mesogloea of the column, that of the mesentery is somewhat swollen and presents pinnately arranged rather short stout processes, those on one side belonging to the longitudinal muscle system, and those on the other to the parieto-basilar. Internally to this swelling the mesogloea becomes thinner and then begins to show on one surface only the muscular elevation belonging to the longitudinal system. These, at first small, lengthen gradually as they are traced outwards towards the inner edge of the mesentery until the largest is reached, when they suddenly diminish, the muscle band internally having a rounded edge, while externally it slopes towards the general surface of the mesogloea. The parieto-basilar muscle is by no means strong.

None of the forms examined, all of which were collected in July, have mature reproductive organs. Immature ova are to be seen, however, partly imbedded in the mesogloea and partly still forming elements of the endoderm layer. These occurred only in the mesenteries of the 2d and 3d cycles.

The species described in the preceding pages seems to agree very well with Lesueur's description of *Actinia annulata* ('17), and I have little doubt as to its identity with that form. Duchassaing and Michelotti do not, however, record it among the forms obtained by them in the West Indies, but, on the other hand, have described a form which they identify with Lesueur's *Actinia solifera*, referring it in their earlier paper ('60) to the genus *Paractis*, and in the later one to the genus *novum Bartholomea* ('66), which is identical with Gosse's *Aiptasia*. It seems probable that *A. solifera* and *A. annulata* are identical, the differences being apparently mainly in coloration. The characters of *A. solifera* as deduced from the various descriptions may be given as follows:—Column cylindrical, elongated, very contractile, marked with longitudinal striæ of a reddish color, and provided with 2–3 rows of small cinclides from which acontia are emitted when the animal is handled. The disc is flat, and the peristome white, with two yellow bands opposite each other (at the gonidial angles, no doubt). The tentacles are very long, decidedly entacmæous, in five or six cycles, and of a brown color annulated with white bands arranged in a broken spiral. When fully expanded the animal measures about 2 cm. in diameter and 10 cm. in length.

The striation of the column is a comparatively unimportant character, since Aiptasias which usually present it have been frequently found without it, or at all events with it so faintly developed as to be hardly discernible, and in forms so extensible as this the size is not a character of sufficient importance to warrant a separation of species. It is possible that Duchassaing and Michelotti's *A. solifera* is really identical with Lesueur's *annulata*, his *solifera* being really distinct, but it has seemed advisable to unite the two forms and to retain Lesueur's specific name *annulata* as indicating a very evident characteristic.

The octamerous arrangement of the tentacles and mesenteries in *A. annulata* brings up a question as to the validity of Hertwig's tribe Paractiniæ, which was founded ('82) upon single specimens, belonging to two different families, dredged by the "Challenger" from a depth of 1600 and 2160 fathoms respectively. The tribe is characterized by the number of the antimeres not being a multiple of six; in all other respects the two forms which belong to it resemble Hexactiniæ. In one of them, *Sicyonis crassa*, the tentacles and mesenterial pairs are 64 in number; 16 of the pairs of mesenteries are muscular and perfect, 16 muscular and imperfect, and 32 small, only slightly muscular and gonophoric; their formula being evidently 8, 8, 16, 32. Though presenting characters which warrant the formation of a new genus for its reception, yet the number of mesenteries may possibly be abnormal, and the discovery of other specimens show that the hexamerous arrangement is the normal one. There can be no doubt but that the form described here is *Aiptasia annulata* and belongs to the genus to which it is assigned, and this fact lends strong support to the idea that the octamerous arrangement of *Sicyonis* is of much less importance than Hertwig supposed. The other Paractinian, *Polyopsis striata*, possesses thirty-six antimeres, there being thirty-six stomidia representing the tentacles and eighteen pairs of mesenteries. Hertwig thinks it is "most probable that we have here a tetramerous (octamerous?) arrangement of the septa, but that a pair of septa too many has been formed in one interspace on either side." It seems however quite as probable, or even more so, that the arrangement is really hexamerous, only half the mesenterial pairs of the last cycle being developed. Hertwig states that "no arrangement into cycles of unequal values could



be made out," and perhaps the arrangement may be represented by the formula  $6, 6, \frac{1}{2}$  (12). It would seem at all events that further observations are needed to authorize the establishment of the tribe Paractiniæ.

2. *A. tagetes* (Duch. and Mich.), Andr.

*Synon.* — *Bartholomea tagetes*, n.sp. — Duchassaing and Michelotti, 1866.  
*Aiptasia tagetes* — Andres, 1883.

The forms which I refer to Duchassaing and Michelotti's *Aiptasia tagetes* present considerable variation, and I am somewhat doubtful of the propriety of the identification. The various forms of *Aiptasia* resemble each other rather closely, and it seems to be a question if several of the described species are not to be considered merely varieties of one widely distributed species. One of the varieties I include under *A. tagetes* was found only on one occasion, and then in considerable numbers, on a sponge, and these I shall first describe, and then consider a second variety, found upon the under surface of the stones along the shore, and finally refer briefly to a small, evidently young, form found in large numbers in a salt lake celebrated for its brilliant phosphorescence, and situated on the property, on the island of New Providence, known as "Waterloo." It is a shallow lake, bounded at one end by a small mangrove swamp, and connected with the ocean by a narrow channel about a hundred yards in length.

Var. *a. Spongicola*. — Under this designation I shall describe the form found in the sponge. The column measures about 2.5 cm. in length, and in diameter 0.8 cm. ; in a preserved specimen these measurements were respectively 0.7 cm. and 0.6 cm. In color (Pl. I., Fig. 2) the column is pale brownish white, rather darker towards the limbus, and near the margin becoming quite a decided brown marked with opaque white flecks. The disc and tentacles are brown, also flecked irregularly with opaque white, and the peristome and stomodæum are white.

The base is firmly adherent, larger than the column, and sufficiently thin to allow the insertions of the mesenteries to show through. The limbus is very slightly crenate.

The column is cylindrical, tapering slightly towards the top, and provided with a partly double band of cinclides situated on

tubercles, and quite evident. As in *A. annulata* there is considerable irregularity in the arrangement of the cinclides. The wall of the column in some of the preserved specimens is sufficiently thin to allow the insertion of the mesenteries to be seen through it, and I was able accordingly to study the relation of the cinclides to the mesenteries. In one form examined, the arrangement was as follows. Starting with an interspace in which there were two cinclidal tubercles, five spaces destitute of pores followed, the sixth having only one pore; the fourth interspace from this had again only one; the sixth from this, again one; the eighth from this, one; the fourth from this, one; the fourth from this, two; and so on. The arrangement can be better understood from the following scheme:—



Ten series of cinclides were thus present in this specimen, there being for the most part a single pore in each series, only two interspaces possessing two pores. As a rule, a series is situated on each fourth interspace, but there are three exceptions to this: in two cases the series is on the sixth interspace from the one preceding it, and in the third case it is on the eighth, this being probably the result of a series having been omitted. In another specimen I could distinguish only nine cinclidal series, and of these only one or perhaps two consisted of two pores. The relation of the pores to the septa could be made out only for a few series, the arrangement for these being,



Here again between the first and second series one has probably been omitted. In a third specimen I could count only eight series of cinclides, and in this the number of interspaces was in one case eight, in four cases four. In none of the specimens were there twelve cinclidal series, though the numbers given for the last two forms should probably be larger, some of the pores having been no doubt hidden by the contraction and wrinkling of the column wall.

Acontia were observed protruding at the cinclides, at the tips of the tentacles, at the limbus, and even through the base. They were always white.

No sphincter muscle is present. "Yellow cells" are abundant in the endoderm of all the specimens examined.

The tentacles are strongly entacmæous, the length of those of the inner cycle being 0.9 cm., and of those of the outer cycle 0.15 cm. They are arranged in five cycles, their formula being 6, 6, 12, 24, 48, although this arrangement was somewhat obscured by the members of the first two cycles appearing to form only one containing twelve tentacles. The mesogloea of the tentacles, as of the other portions of the body, is thin, and this is characteristic of all the species of this genus that I have studied. The muscles of the tentacles are simple and only slightly developed. On account of the absence of a circular muscle the tentacles are not infolded in contraction.

The mesenteries are in four cycles arranged thus (Pl. III., Fig. 3): those of the first cycle (I.) only are complete, those of the second (II.) are large and well developed, those of the third (III.) quite small and apparently without mesenterial filaments, and those of the fourth (IV.) are minute processes of the mesogloea of the column which do not project beyond the surface of the endoderm. The formula of the mesenteries is 6, 6, 12, 24. The number of the stomata present was not made out with certainty, but there appeared to be two, situated as in *A. annulata*, an outer and an inner one. The longitudinal muscle bands are developed in the mesenteries of the first and second cycles; they occupy a considerable portion of the surface of the mesenteries, their elevation gradually diminishing towards the inner edge. The bases of all the mesenteries are dilated somewhat, but in those of the first and second cycle there is no pinnation of the dilated portion, while in the small and poorly developed mesenteries of the third cycle it was present. The parieto-basilar muscle is very weak. The reproductive organs were confined to the mesenteries of the second cycle. All the specimens examined were males with mature or nearly mature spermatozoa.

Var.  $\beta$ . *Castanea*. — This variety was found not very abundantly upon the under surface of blocks and fragments of coral rock along the shores. The color of the column is pale reddish



brown, with lighter longitudinal striæ marking the lines of insertion of the mesenteries. The disc and tentacles are brown, flecked with opaque white patches. The peristome and stomodæum are white, or in some cases the peristome is brown, slightly paler than the disc, and flecked with white spots.

The base adheres firmly, and is slightly larger than the column, measuring about 1.4 cm. in diameter. It is thin enough to allow the insertions of the mesenteries to be seen through.

The column is cylindrical and contractile, measuring about 1.5 cm. in height and 0.9 cm. in diameter. The cinclides are not very distinct in the living animal, although in preserved specimens they stand out as tubercles quite as distinctly as in the other variety, being arranged very much in the same manner as in it. In one specimen the numbers in the various series, as far as could be made out, ran thus: 1, 1, 1, 2, 1, 2, 1, 2, 1, 1. Acontia were emitted with comparative readiness, and were always white. There is no sphincter muscle, and the endoderm contains "yellow cells."

The tentacles are very entacmæous, and are arranged in four cycles, their formula being 12, 12, 24, 48. The length of those of the inner cycle is 1.2 cm., and of those of the outer cycle 0.75 cm. As in variety *a*, they are all smooth, cylindrical, and pointed, and on account of the absence of a circular muscle are not infolded in contraction.

The description given of the arrangement of the mesenteries of variety *a* applies equally well for this variety, the only difference being that the internal edge of the longitudinal muscle bands ends more abruptly (Pl. III., Fig. 2). I did not succeed in observing the stomata.

Reproductive organs are present only on the mesenteries of the second cycle. In the specimens examined only ova were present; and they were not quite mature.

*Young Form.*—This was obtained in considerable numbers on the grass along the shores of the lake mentioned above, and I was at first inclined to consider it a distinct species; but further study has led me to place it here as a young form of *A. tagetes*. In coloration it agrees closely with variety  $\beta$ , just described, the column being brown with longitudinal striæ indicating the insertion of the mesenteries. Above the color becomes deeper, and in this darker region the column is flecked

with opaque white. The tentacles and disc are brown, also flecked with opaque white; and the peristome is white.

The base is firmly adherent and somewhat larger than the column. The latter measures from 0.5–1 cm. in height and from 0.3–0.4 cm. in diameter, and is provided with a single row of cinclides situated on tubercles, and six in number. They are colorless and transparent, so that they are quite conspicuous. No trace of a sphincter muscle could be seen; and as in the forms already described, the "yellow cells" were abundant in the endoderm.

The tentacles are entacmæous, and in four cycles, their formula being 6, 6, 12, 24. The length of those of the inner cycle is about 0.4 cm.

The mesenteries are arranged in three cycles. Of these, the first is perfect; the second, imperfect and small, and not provided with mesenterial filaments; while the third is represented by the merest rudiments of processes from the mesogloea of the column wall. In one specimen examined there was a difference in the mesenteries of the two halves of the body. In one half there were three perfect pairs of mesenteries, and in the other, four, the secondary and tertiary cycles being arranged correspondingly. I could not discover the mesenterial stomata, nor a parieto-basilar muscle. The longitudinal muscle bands of the perfect mesenteries cover only a comparatively small portion of the surface of the mesentery, and end abruptly internally, as in variety  $\beta$ .

In none of the specimens examined were there any traces of reproductive organs, as might be expected from the slight development of the mesenteries of the second and third cycles.

My reasons for at first supposing this form to be a distinct species were its occurrence in such large numbers, all being about the same size, and the failure to obtain any larger specimens, resembling varieties  $\alpha$  or  $\beta$ , from the lake. A careful examination of the shores and deeper portions of the lake was not made; and it is probable that adult specimens of variety  $\beta$  may be found there, in the deeper water, a little way out from the shore, the shallower water and the grass abounding there, with the myriads of copepods swimming about among it, affording more suitable conditions for the growth of the young forms. There can be no doubt but that the specimens are young, and

the similarity of coloration inclines me to the belief that they belong to variety  $\beta$ .

Duchassaing and Michelotti state that *A. tagetes* is characterized by the presence of a double row of cinclides, indications of a third imperfect row being usually present. It differs in this respect from the form I have just described; but it also fails to agree with the figure they give of the species ('66, Pl. VI., Fig. 16), which is represented with a perfect row above, and below this a second imperfect row. The *Aiptasia* (*Bartholomea*) *inula* of the same authors is said to have only a single row, and in this perhaps agrees more nearly with my specimens; but I do not consider that an identification with that form would be as satisfactory as that employed.

The species was originally described from specimens obtained at Porto Rico and St. Thomas, and probably ranges throughout the West Indies. It seems to be rather closely related to the *A. pallida* of the Eastern coast of North America, and may prove to be identical with it, and also bears considerable resemblance to *A. saxicola*, judging from Andres' description of that form ('83).

#### Family Antheadæ, Hert.

*Synon.* — Actinines vulgaires (pars) — Milne-Edwards, 1857.

Actiniadæ — Gosse, 1858.

Actiniadæ (pars) + Antheadæ (pars) — Gosse, 1860.

Actininæ (pars) — Verrill, 1868.

Antheadæ — R. Hertwig, 1882.

Actinidæ + Cereactidæ — Andres, 1883.

Actininæ adhering to foreign bodies by a flat contractile base. Column usually smooth, occasionally verrucose towards the upper part, without cinclides. Margin frequently provided with acrorhagi, but may be smooth. Tentacles numerous, long, cylindrical, and smooth. Sphincter muscle only slightly developed, diffuse. Perfect mesenteries numerous, and all, except the directives, gonophoric. No acontia.

The synonymy of this family as defined above is somewhat complicated. Milne-Edwards' division of Actinines vulgaires ('57) contains certain forms (*e.g.*, *Paractis*, *Corynactis*) which must be referred to other families, and is consequently not quite comparable to the Antheadæ as limited above. Gosse's family,



Actiniadæ, however, agrees closely; but in his larger work ('60) he separated it into two families,—the Antheadæ, characterized by possessing no acrorhagi, and the Actiniadæ, which did possess them. Of the forms which he included under the former family, *Aiptasia* has already been shown to be a Sagartid; *Anthea* (*A. cereus*) has been shown to possess acrorhagi, which are not, however, conspicuously colored; the *Actinia pustulata* of Dana is a *Phymactis*; and *Actinopsis* has been referred by Andres ('83) to an entirely different family. The three genera referred to the Actinidæ suffer a similar dispersion, the genus *Actinia* being the only one which truly belongs to the family. Verrill in his earlier papers adopted Gosse's arrangement, but subsequently united the two families under the term Actininæ, including, however, certain forms which should certainly be separated. Andres likewise unites *Anthea* and *Actinia* in one family, but established another, Cereactidæ, for a form not possessing acrorhagi. This I do not consider necessary, since, as will be shown, the internal structure of the members of the genus *Cereactis* (*Condylactis*) is similar to that of the *Antheas* and *Actinias* so far as is known.

Gosse's original name, Actiniadæ, would perhaps be preferable to that employed, since the generic term *Anthea* ought apparently to be replaced by *Anemonia*, which has the priority. On account of its similarity, however, to the term employed to designate the sub-tribe, but especially since Antheadæ has already been used by R. Hertwig ('82) with the same limitations as are applied to it here, I have thought it well to retain the latter name.

#### GENUS CONDYLACTIS, Duch. and Mich.

*Synon.*—*Actinia* (pars)—Auct.

*Condylactis*—Duchassaing and Michelotti, 1866.

*Cereactis*—Andres, 1883.

Antheadæ, with the column smooth or slightly verrucose towards the upper part. Margin elevated slightly, so as to form a collar; not provided with acrorhagi.

3. *Condylactis passiflora*, Duch. and Mich. (Pl. I., Fig. 3; Pl. III., Figs. 4–6.)

This is one of the most abundant and striking forms obtained. It was found in considerable numbers on the under surface of

overhanging ledges, or in depressions or cavities in the coral rock; it is also one of the forms figured by Uhthoff as occurring at Green Turtle Cay. It seems tolerably certain that the form described by Duchassaing and Michellotti from St. Thomas as *Condylactis passiflora* is identical with the Bahaman form under consideration. The description given by those authors, however, is far from perfect, and presents certain differences from what I find in the Bahama specimens, which are, however, I think, capable of explanation. A discussion of this point will, however, be deferred until a description of the specimens studied has been given. I would merely point out here that Andres' generic term *Cereactis* must be replaced by *Condylactis*, which has the priority.

The column is usually bright scarlet in color, becoming somewhat brownish above; the disc is pale brown, and the tentacles are of the same shade, usually tipped with crimson, and assuming when contracted a somewhat greenish hue. In some cases the crimson tips are wanting. The color of the column varies somewhat; occasionally it is somewhat darker, more brownish, than in the specimen figured; in other cases the coloring matter is arranged in closely approximated minute dots, and in others, again, it is uniformly distributed, but much paler, varying to orange, or even yellow.

The base is firmly adherent and somewhat larger than the column. The limbus is crenated. The column varies considerably in the amount of extension, the same individual measuring, when fully extended, about 11 cm. in length and 3.75 cm. in diameter; while when in the condition which may be termed expansion it measures only 7 cm. in height by 6.3 cm. in breadth. In the preserved specimens the height is about 4 cm. and the diameter 5.5 cm. In adults the column is apparently smooth, but in smaller individuals it is furnished in its upper part with small, irregularly scattered verrucæ, which, however, do not seem to be as adhesive as they are in *C. aurantiaca*, according to Andres. The sphincter muscle is only very slightly developed, and is of the diffuse type (Pl. III., Fig. 4), and, consequently, the infolding of the tentacles during contraction is by no means perfect. The mesoglœa of the column wall is comparatively thick, measuring about 0.17 mm. The endoderm is richly supplied with "yellow cells."

The margin is crenate, the indentations corresponding to the insertions of the mesenteries. It is somewhat elevated, so as to form a slight collar, separated by a naked area from the tentacles. These are smooth, cylindrical, and only slightly entamæous. They are 96 in number, and are arranged according to the formula, 6, 6, 12, 24, 48, although they appear to be in four cycles only. Pores are present at their extremities, as was shown by the jets of water which issued therefrom when the animal was induced to contract suddenly, but I was unable to demonstrate any openings in my sections. The ectodermal muscles are arranged on well-marked elevations of the mesogloea (Pl. III., Fig. 5), which occasionally, but not very frequently, anastomose, thus enclosing a number of muscle-cells within the mesogloea. The disc is concave and smooth, and considerably broader than the column, measuring in the extended condition 11 cm. in diameter, and in the expanded condition about 18 cm. The ectodermal muscles are arranged similarly to those of the tentacles. The mouth is large, and the peristome not markedly elevated. The gonidia are large and prominent, and colored similarly to the disc.

There are 12 perfect mesenteries, 12 which are attached to the stomodæum for about half its length, but are free below, and 24 which are quite imperfect, or united to the stomodæum only to a very slight extent. The longitudinal and parieto-basilar muscles are well developed, a characteristic of the former being the difference in the length of the various mesogloéal processes, whereby the bands have a sinuous outline in transverse sections (Pl. III., Fig. 6). The mesenteries of all the cycles, with the exception of the directives, are gonophoric. Only the inner mesenterial stomata are present.

The points in which Duchassaing and Michelotti's description of *Condylactis passiflora* ('66) differs from the specimens obtained by me are principally that these authors state that the column is provided with "tuberculis parvis sparsis numerosisque," and, secondly, they do not describe the tentacles as possessing crimson tips. As regards this latter point, as stated above, I obtained some specimens in which this striking coloration of the tentacles was wanting. The absence of the tubercles seems, however, more important. In the figure which Duchassaing and Michelotti give ('66, Pl. V., Fig. 7) they are represented as



minute points scattered irregularly over the column; and I am inclined to believe that these authors had to do with a specimen in which the coloring matter was distributed in minute dots over the surface of the column, in which case, as I can testify from experience, the appearance is strongly as if the column was covered by exceedingly minute scattered tubercles. In other respects, judging both from the description and from the figure, the correspondence to the Bahama specimens is so great as to allow of little doubt of their identity with the St. Thomas forms.<sup>1</sup>

*C. aurantiaca* (D. Ch.), the *Cereactis aurantiaca* of Andres ('83), is certainly closely related to *C. passiflora*, but differs sufficiently to constitute another species. The most important difference lies in the absence of the verrucæ in the adult *passiflora*; while in *aurantiaca*, according to Andres, they are very evident, being of a pure white on a brownish ground, and tolerably large. A nearer relation is apparently to be found in the *Paractis erythrosoma* of Klunzinger ('77), which inhabits the Red Sea. This form, originally discovered by Ehrenberg ('34), was referred by him to the genus *Actinia* (*Isacmæa*); Klunzinger, however, transferred it to the genus *Paractis* on account of its possession of a margin raised so as to form a collar; and Andres placed it among the doubtful forms belonging to the genus *Anemonia*, regarding it as related to *A. sulcata*. I have little doubt but that this form is to be referred to the genus *Condylactis*, and that its correct appellation is *C. erythrosoma* (Ehr.). It agrees in many particulars with the Bahama specimens, and I am almost inclined to consider the two forms identical; but on account of the absence of any information as to the internal anatomy of the Red Sea form, I have thought it better to separate them. In the absence of verrucæ, and in the general coloration, the resemblance is very striking. In some details of the coloration, however, such as the greenness of the tentacles and in the size, differences, not very important certainly, are to be noticed.

If Andres' description of the genus (founded upon a single

<sup>1</sup> In a preliminary notice of this paper, which was published in the *Johns Hopkins University Circulars*, Vol. VIII., No. 70, I referred to this form as *Cereactis Bahamensis*, n. sp., indicating, however, its probable identity with *Condylactis passiflora*. I have since become convinced of the correctness of such an identification.

species) be accepted, *C. passiflora* will be excluded from it. The presence of verrucæ, which Andres makes of so much importance, cannot, it seems to me, be considered a generic characteristic, since in the Bahama specimens they are present in young individuals, but disappear in the adults. Since, then, the Bahama species agrees so closely in other particulars with the European form, I have given the definition of the genus so as to include forms both with and without verrucæ.

Family Bunodidæ, Gosse.

*Synon.* — Actinines verruqueuses — Milne-Edwards, 1857.

Bunodidæ — Gosse, 1860.

Cerææ — Duchassaing and Michelotti, 1866.

Bunodinæ — Verrill, 1868.

Tealidæ — R. Hertwig, 1882.

Actininæ adhering to foreign bodies by a flat contractile base. Column occasionally smooth, but usually provided with tubercles either simple or compound. No cinclides. Sphincter muscle is strong and circumscribed. Perfect mesenteries usually numerous, those of the first cycle, with the exception of the directives, being gonophoric. No acontia. Tentacles smooth, cylindrical, and entacmæous.

Gosse, who established this family, laid most stress on the presence of the tubercles, and this has usually been considered the characteristic of the family, though later authors have added the character of the absence of acontia, thus excluding from the family a single species, *Bunodes coronata*, which was included by Gosse. The true relationships of this form have already been referred to. Hertwig's original objection ('82) to the term "Bunodidæ" is based upon this error of Gosse, and he has since ('88) withdrawn his name Tealidæ in favor of the older one. He was, however, the first to point out the systematic value of the well-developed circumscribed sphincter muscle, and to make this and the absence of acontia two important characteristics of the family, at the same time lessening the excessive importance of a tuberculated column by including a genus, *Leiotelia*, in which the column wall is smooth. The presence of a large number of perfect mesenteries is also an important characteristic; but in one genus at least, as I shall show, this feature is wanting.

## Genus BUNODES, Gosse.

Bunodidæ with the column provided with tubercles arranged in vertical series, of which either all reach the limbus, or only those corresponding to the primary tentacles, in which case the other series stop at varying distances from the margin according to their importance. Margin tuberculate, and forming a more or less distinct collar. Tentacles polycyclic and entacmæous. Twelve pairs of perfect mesenteries.

The limitations of this genus have already been indicated.

4. *Bunodes tæniatus*, n. sp. (Pl. I., Fig. 4; Pl. III., Fig. 7.)

The single specimen of this species which I obtained was found on the under surface of a block of coral rock in the bay to the westward of Nassau. The color of the column is olive green; the tubercles with which the column is covered are of two different colors, arranged so as to form twenty-four longitudinal bands. Twelve of these, each containing five vertical rows of tubercles, are of the same color as the column, the other twelve, each containing three vertical rows of tubercles, being more yellowish. The acrorhagi are also yellowish, while the tentacles are gray with transverse oval blotches of opaque white on their inner surfaces. The disc and peristome are olive green.

The base is strongly adherent and somewhat larger than the column, which measured about 3.2 cm. in height in the fresh condition, the diameter being about the same; in preserved specimens the height is about 1.5 cm. The entire surface of the column is covered with tubercles disposed in vertical rows, and placed so closely as to allow the general surface of the column wall to be seen only with difficulty. There are altogether 96 rows of these tubercles, all of which extend from the margin, which is provided with acrorhagi, to the limbus, and there is little, if any, difference in the size of the tubercles in the various rows. In structure the tubercles are markedly different from the verrucæ which are to be found in *Aulactinia* (see below), and resemble very closely the acrorhagi. In fact, the figure given by the Hertwigs ('79) of the acrorhagi of *Anthea cereus* would almost answer for a figure of the tubercles of *Bunodes*, except that the nervous layer is not so readily seen in the latter,



and the tubercles project more above the general surface. They are simply batteries of nematocysts, the presence of these bodies at once distinguishing them from the verrucæ of *Aulactinia*, etc.

R. Hertwig ('82) has stated his objections to the presence or absence of elevations of the column wall being considered of systematic importance except in so far as genera and species are concerned. That these objections must be sustained is certain; but it also seems probable that more attention ought to be paid to the structure of the elevations than has hitherto been done. It is possible to distinguish in them at least three varieties: (1) simple elevations of the mesoglœa unaccompanied with any extensive modification of the ectodermal epithelium, e.g. *Bunodes gemmacea* according to Jourdan ('80), and *Bunodes (Cylista) minuta*, R. Hertwig ('82); (2) evaginations of the entire column wall furnished with numerous nematocysts, as in the acrorhagi of *Anthea*, etc., and the tubercles of *Bunodes tæniatus*; and (3) verrucæ in which the ectoderm consists of peculiar elongated cells, quite different from those of the column wall in general. Jourdan, in his description of the tubercles of *Bunodes gemmacea*, apparently considers them to be produced by the dipping down of the ectoderm between them into the mesoglœa to form what he terms "verrues glandulaires." R. Hertwig has, however, shown by his observations on *Bunodes (Cylista) minuta* ('82) that Jourdan's interpretation of the appearance presented by his sections was erroneous, and has maintained that these apparent ectodermal enclosures within the mesoglœa were produced by the contraction of the column wall of the specimen examined, whereby deep pleatings were produced which "may look like detached epithelial islands in transverse section." This being the case, the elevations of *Bunodes gemmacea* belong to the first of the three groups enumerated above, and are markedly different from those of *B. tæniatus*.

The sphincter muscle (Pl. III., Fig. 7) is very strong, forming a large projection into the body cavity. In transverse section it has a more or less circular outline, and is attached to the column wall by a pedicle of mesoglœa which has a fenestrated appearance, containing numerous cavities lined with muscle cells. From this pedicle the mesoglœa processes arise in a very irregular manner and anastomose in all directions, so that the central portion of the muscle thickening appears to have a

reticular structure, there being here and there areas of mesogloea of varying size. Towards the exterior the mesogloéal processes cease to anastomose, and run radially toward the surface of the thickening. The thickening thus appears to be composed of two parts passing gradually into each other, a central part of reticular structure, and a peripheral part composed of mesogloéal processes arising and radiating out from the reticular portion. The muscular layer throughout the rest of the column is weak, and the mesogloéal layer is comparatively thin. The endoderm throughout contains numbers of "yellow cells" and a dark pigment which persists in preserved specimens, and is therefore not soluble in alcohol nor destroyed by weak nitric or chromic acids.

The margin is furnished with acrorhagi, slightly tuberculate upon their outer surfaces; they are simply the enlarged uppermost turbercles. The tentacles are not very long, the inner ones measuring about 1.9 cm. They are entacmæous, cylindrical, and arranged in five cycles, their formula being 6, 6, 12, 24, 48, there being thus 96 in all. In cross section the thinness of the mesogloea and the absence of any muscular processes are noticeable.

The ectodermal musculature of the disc is not particularly strong, the mesogloea being raised into processes of no very great height. There are no enclosures of muscle cells in the mesogloea as in *Tealia crassicornis*.

There are altogether 48 mesenteries, and of these 24 are perfect and 24 imperfect; 12 of the perfect ones, however, are not attached quite so far down the stomodæum as the other 12, to which latter series the directives belong. The longitudinal and parieto-basilar muscles are present, but show no peculiarities calling for special mention, except that the former are by no means so prominent as in *Tealia crassicornis* or *bunodiformis*. All the mesenteries, with the exception of the directives, are gonophoric. I was not able to discover any mesenterial stomata, though it appeared as though the inner ones were present.

Before I had concluded my study of this form I felt inclined to identify it with the European *B. gemmacea*. The extension of the geographical area inhabited by that species by such an identification seemed a much slighter obstacle than certain structural discrepancies, some of which, however, seem to be in-

cluded in the variations which the species presents. For instance, in *B. gemmacea*, as figured by Gosse ('60) and Andres ('83), the tubercles do not as a rule all reach the limbus, but only those of the primary series. In Figure 2 of Gosse's Plate IV. the arrangement is similar to what occurs in the Bahama specimen, so that this difference may be overlooked. Again, in most cases it is only the primary tubercles which are lighter in color; but Gosse states that "sometimes, however, the quaternary row which bounds each primary on each side is also white," and he figures such a condition in Pl. IV., Fig. 3. If one imagines a form with the rows of tubercles all reaching the limbus, and having not only the primary tubercles, but also the quaternaries on either side, light colored, — a combination, in fact, of the two varieties figured by Gosse, — we would have a near approach to the condition of the Bahama form. But there is still another difference. In the European Gem there are only six light-colored bands, whereas in the form I have described these are twelve in number. This seems a serious discrepancy; but an approach towards such a condition is to be found in the European forms. In these the warts of the secondary series are usually somewhat paler than those of the tertiary series, and if the paleness should become as marked as in the primary series, and have extended so as to include the series on either side, we should have the arrangement which is found in the Bahama specimen. The presence of a fifth series of tubercles, or, in other words, of 96 series of tubercles, seems to be a more important character than that of the coloration. In the European forms apparently the number of series is invariably 48; but whether this is sufficient for the establishment of a new species seems to me doubtful. The discrepancies of coloration, too, may be dependent upon the presence of the extra series of tubercles.

Even allowing, however, these possibilities, *B. teniatus* must be considered a decidedly aberrant variety. I have thought it advisable, however, to consider it a distinct species, particularly on account of the difference in the structure of the tubercles, which has been referred to above. The erection of a new species from the study of a single specimen is usually a dubious matter, and it is quite possible that the examination of a number of specimens, and a further study of the histological structure of the tubercles of *B. gemmacea* will necessitate the union of the two forms.



The form described by Lesueur ('17) from St. Vincent as *Actinia bicolor* has been assigned by Gosse ('60) to the genus *Bunodes*. In coloration it resembles *B. tæniatus*, the column being "divided longitudinally with brown and white bands," and the tentacles having "a row of white spots on the superior part." In other respects, however, there appear to be decided differences, and, judging from Lesueur's description, his *A. bicolor* should be assigned to the genus *Adamsia*, as has been done by Andres ('83). The limbus only is furnished with tubercles, of which, however, there are several rows; and in habit also it resembles the members of the genus *Adamsia*, being found adhering to shells.

There seems to be a good deal of probability that *B. tæniatus* is simply a color variety of Lesueur's *Actinia granulifera* ('17), which has been variously referred to the genera *Aulactinia*, *Oulactis*, and *Anthopleura*. Among the forms figured by Uthoff, from Green Turtle Cay, is one evidently identical with Lesueur's species. I did not find any specimens similar to that from Green Turtle Cay with which to compare my *B. tæniatus*, and accordingly prefer to consider it distinct for the present. I have no doubt but that Lesueur's *A. granulifera* is a *Bunodes*.

#### Genus AULACTINIA, Verr.

*Synon.* — *Actinia* (pars) — L. Agassiz, Ms., 1849.

*Aulactinia* — Verrill, 1864.

Bunodidæ, with the upper portion of the column provided with longitudinal rows of verrucæ, the lower portion being smooth. The margin forms a more or less distinct collar, and the tentacles are polycyclic and entacmæous. The six pairs of mesenteries of the first cycle are alone perfect.

Verrill, who first defined this genus, seems to have placed too much importance upon the lobation of the upper verrucæ, which were considered acrorhagi, and in this Andres has followed him. The essential peculiarities of the genus, as it is understood here, are the limitation of the verrucæ to the upper part of the column, and the small number of perfect mesenteries. This latter characteristic I have found to hold in *A. capitata*, the type species of the genus.

5. *Aulactinia stelloides*, n. sp. (Pl. I., Figs. 5-6; Pl. III., Figs. 8-10.)

This form was found usually buried up to the tentacles in the sand in tidal pools, but also not unfrequently on the under surface of blocks of coral rock along the shore in shallow water. In color the column (Pl. I., Fig. 5) is brown, darkening above, and pale, and, in some cases, almost colorless below, the lines of the insertions of the mesenteries being usually evident. The verrucæ, on the upper part of the column, are pale, almost white. The tentacles are brown, or almost cream-colored, and are banded or mottled upon their inner surfaces with white, which sometimes varies to olive-green. Disc (Pl. I., Fig. 6), olive-green, with a zig-zag band of white about midway between the bases of the tentacles and the mouth. In a small specimen the tentacles were almost white, their mottlings being opaque white, and in this case the disc also was almost white, with only a faint indication of green.

The base is rather strongly adherent and somewhat larger than the column, measuring about 1.3 cm. in diameter. The column is cylindrical, measuring in the fresh condition 1.7 cm. in height and 1.1 cm. in diameter; in the largest of the preserved specimens these measurements are about 0.8 cm. and 1.1 cm. respectively. The lower portion is smooth, while the upper one-third is provided with vertical rows of verrucæ, to which particles of sand, etc., adhere. The upper verrucæ are more prominent than those lower down, the marginal ones being the largest of all, but showing no indications of lobation. Structurally the verrucæ are elevations of the entire column wall, the ectoderm, mesogloea, and endoderm being, as it were, blown out at certain spots to form hemispherical elevations (Pl. III., Fig. 8). The mesogloea, in the centre of the verrucæ, is quite smooth on both surfaces, but around the margin its endodermal surface is raised into rather strong finger-like processes (*mp*), covering which are the endodermal muscle cells. The ectoderm of the central portion (*mcc*) is markedly different from that found at the margins and on the column wall generally; it is composed apparently altogether of exceedingly fine, almost filiform cells, there being none of the claviform gland cells elsewhere abundant, and apparently no "stutzzellen." It is difficult to separate these cells from the mesogloea by macera-

tion, the ordinary ectoderm cells surrounding them being on the other hand easily separable, a fact which has been observed by von Heider ('77) as characteristic of the similar cells of the verrucæ of *Heliactis*. The histological structure of verrucæ will be discussed more fully later on under *Phymanthus crucifer*, where they are well developed and suitable for investigation.

The sphincter muscle is strong and of the circumscribed type (Pl. III., Fig. 9). The mesogloæal processes supporting the endodermal muscles become somewhat stronger as they approach the region of the circular muscle, and then suddenly become much elongated and branched, forming a ridge almost circular in cross section, projecting into the body cavity. There is no distinct pedicle from which the processes take a common origin, as in other Bunodidæ which have been examined, but most of the processes arise independently from the mesogloæa layer, only those towards the inner part of the thickening arising from a common lamella, or process, which, however, is thin, and not at all pedicle-like. "Yellow cells" are everywhere abundant in the endoderm.

The margin is somewhat raised, forming a collar, a bare space intervening between it and the bases of the outermost tentacles. It bears the uppermost of the verrucæ, which, as already stated, are not lobed and do not present any difference of structure from those found on the column. The tentacles are cylindrical and decidedly entacmæous, the inner ones measuring 1.7 cm. in length, and the outer 0.8 cm. They are 48 in number, being arranged in four cycles, thus: 6, 6, 12, 24.

The mesenteries are arranged in five cycles, only those of the first cycle being complete (Pl. III., Fig. 10), and of these the directives are united to the stomodæum to a greater extent than the others, the lips of the gonidial grooves being prolonged downwards to form languettes with which the directives are united. The mesenteries of the second cycle (II.) are nearly if not quite as well developed as those of the first cycle, but are all imperfect; those of the fourth cycle (IV.) have well-developed muscle bands, but no mesenterial filaments; while the members of the fifth cycle (V.) are very diminutive, not projecting beyond the surface of the endoderm, and in the specimen examined, were not present in certain interseptal spaces where they should have occurred, the cycle being thus incomplete. The



rudimentary nature of this last cycle is also evidenced by the absence of a fifth cycle of tentacles, there being usually one cycle of tentacles more than mesenteries. I do not think that the small size and incompleteness of these mesenteries are due to the specimens examined being young, but rather imagine that there is a tendency towards the disappearance of this cycle in this form.

The inner mesenterial stomata only were observed. The muscle bundles, both longitudinal and parieto-basilar, are present, and fairly well developed. In one specimen examined, one mesentery of a pair belonging to the first cycle had longitudinal muscle fibres equally well developed upon both its surfaces, the parieto-basilar being absent, and a greater portion than usual of the surface of the mesentery was covered with muscle fibres. The reproductive organs are borne by the mesenteries of the first and second cycles (Pl. III., Fig. 10), with the exception of the directives. On some of the mesenteries of the second cycle they were absent; but no regularity was apparent in their occurrence or absence on different mesenteries of the cycle.

This form seems to resemble in some respects *Bunodes stella*, Verrill ('64), and I regret that my efforts to obtain specimens of that species for comparison were unsuccessful. Andres ('83) places it among the "Bunodidæ incerto sedis," being uncertain whether to consider it a *Bunodes*, *Phymactis*, or *Aulactinia*. Perhaps further investigation will demonstrate the identity of the two forms, in which case they should both be included under the name *Aulactinia stella*.

In placing *Aulactinia* among the Bunodidæ, the importance of one of the fundamental peculiarities of the family as defined by R. Hertwig ('82), viz., the presence of numerous perfect mesenteries, has been lessened. I was at first inclined to separate *Aulactinia* from the Bunodidæ on account of the small number of perfect mesenteries which they possess, but further consideration showed the inadvisability of such a classification, since in other important features, such as the presence of a strong circumscribed endodermal muscle, of reproductive organs on the mesenteries of the first cycle, and in the absence of cinclides and acontia, there is agreement. The small number of perfect mesenteries does not seem to be a character of sufficient impor-

tance to warrant the establishment of a new family, since in the Bunodidæ which have been examined there is considerable variation in the number of mesenteries which reach the œsophagus. Thus in *Tealia crassicornis*, according to the Hertwigs ('79), all the mesenteries, of which there are over 100, reach the œsophagus, while in *Leiotelia nymphaea*, in which the mesenteries are arranged in six cycles, only those of the first three cycles, *i.e.* twenty-four, are perfect, and in *Bunodes tæniatus* we have seen that twelve of the twenty-four perfect mesenteries were not attached to the œsophagus throughout its whole length. *Aulactinia* may be regarded as the one extreme in the number of perfect mesenteries, and *Tealia crassicornis* as the other.

The verrucal nature of the ectodermal elevations may perhaps be of considerable importance from a systematic point of view, but this point has been already alluded to.

#### Sub-tribe DENDROMELINÆ.

Hexactiniæ with the tentacles simple and arranged in cycles on the margin. The upper part of the column immediately below the margin provided with dendritic processes (pseudo-tentacles). Base adherent.

This sub-tribe is established for the reception of two very remarkable genera, *Lebrunea*, occurring in the West Indies in shallow water, and *Ophiodiscus*, obtained by the "Challenger" in deep water (2160 and 1375 fathoms) in the Southern Pacific. The specimens of the latter genus were unfortunately in a very imperfect condition when examined by R. Hertwig, who described them ('82), and the only evidence of the existence of the peculiar processes which form the characteristic feature of the group was a single, delicate, short-stemmed, much-branched structure, enclosed in the same piece of cloth as the four specimens of the genus that were obtained. It was found quite unattached to any of the specimens, and presumably had been torn away by the rough treatment the specimens appeared to have suffered, no doubt from the dredge. The coelenterate nature of this structure is almost certain, and that it belonged to the specimens with which it was enclosed seems equally so, and, though absolute certainty is wanting, yet it seems proper to associate the Ophiodisci with *Lebrunea*. The peculiar form

*Eumenides ophiseocoma* described by Lesson ('28) for New Guinea may, perhaps, be distantly related to the forms referred to this sub-tribe, but differs in so many points that it cannot be included with them.

Hertwig associated *Ophiodiscus* with the Paractinidæ, which belong to the sub-tribe Actininæ as defined in this memoir, on account of the circular muscle being imbedded in the mesogloea, at the same time holding open the question as to the propriety of erecting the genus into a special family. Since the various sub-tribes are characterized by the nature of the tentacles, and since the possession of the peculiar pseudo-tentacles, to employ the name Hertwig has applied to them, is so characteristic, I have thought it well to establish for the two genera, not merely a new family, but a new sub-tribe, making the division which they constitute of equal importance to the Stichodactylinæ or Thalassianthinæ. This sub-tribe is probably more nearly allied to the Actininæ than to the other sub-tribes of the Hexactinidæ, since the tentacles are arranged in cycles and not radially, and are simple and conical. Their situation on the margin is an important point, however, which in addition to the possession of pseudo-tentacles distinguishes the sub-tribe from that of the Actininæ, and associates it, to a certain extent, with the Stichodactylinæ, in many of which the simple tentacles are marginal in position. Duchassaing and Michelotti considered the genus *Lebrunea* to be close to *Phyllactis*, but such an alliance is unquestionably erroneous. The pseudo-tentacles have no relationship either in position or structure to the fronds of the Phyllactidæ.

The separation of the two genera, *Lebrunea* and *Ophiodiscus*, in distinct families will probably be found necessary eventually, inasmuch as the differences between them, such as the presence in one and the absence in the other of a circular muscle, and the specialization of the mesenteries into muscular and gonophoric cycles in *Ophiodiscus*, are probably of more than generic importance. But until a greater number of forms belonging to the group have been discovered, and their structure thoroughly studied, the establishment of separate families seems unnecessary.



Genus *LEBRUNEA*, Duch. and Mich.

*Synon.*—*Lebrunea*—Duchassaing and Michelotti, 1860.

Base firmly adhering to foreign bodies; tentacles in several cycles; pseudo-tentacles, six in number, dichotomously branching; no sphincter muscle, and no specialization of muscular and gonophoric mesenteries.

6. *Lebrunea neglecta*, Duch. and Mich. (Pl. I., Fig. 7; Pl. III., Figs. 11-14.)

*Synon.*—*Lebrunea neglecta*—Duchassaing and Michelotti, 1860.

Two specimens of this species were obtained at the Bahamas, both of which were discovered by members of the Laboratory, who were engaged in making collections for the University of Pennsylvania. Dr. Charles Dolley, who was in charge of the collections, kindly allowed me to make a drawing of one of the specimens, and on my return generously placed it at my disposal for detailed examination. The opportunity thus presented of examining such an interesting form, I eagerly accepted, and I desire here to offer to Dr. Dolley and his assistant, Mr. M. Greenman, my sincere thanks for their courtesy. The other specimen obtained is in the Museum of the University of Pennsylvania.

Like those obtained by Duchassaing and Michelotti at St. Thomas, the Bahama specimens were found attached to the banks of coral rock near the shore. In color our specimens differed somewhat from those obtained by the authors just mentioned, whose description I here quote: "Corps cylindrique, plissé transversalement, à couleur bleuâtre avec des taches blanches, de 1-2 pouces de hauteur. Disque large de 6-7 lignes; bouche grande et blanchâtre; tentacules subégaux et à peu près de même longueur que le diamètre, colorés en rougeâtre dans leur moitié inférieure, et blanc dans la reste de leur étendue. La couleur bleuâtre des appendices change et devient jaunâtre aux dernières ramifications." The specimen I examined was colored as follows (Pl. I., Fig. 7): Column purplish brown; pseudo-tentacles seal-brown, the ultimate ramifications being white. Disc and tentacles paler brown, the latter being whitish at the tips. The disc was transparent, allowing the

yellowish mesenterial filaments to show through, and was marked with six paler lines radiating from the mouth towards the bases of the tentacles of the first cycle. Peristome white, with the gonidia a more opaque white.

The base is firmly adherent, apparently slightly larger in diameter than the column, measuring 2.5 cm., at least so it is in the preserved specimen, it being impossible to see either it or the column in the fresh specimens owing to the position of the tentacles. The column in these latter measured about 2.9 cm. in height; in the preserved specimens the height was 2 cm., and the diameter about the same. The surface of the column is thrown into transverse folds, and a close examination shows numerous minute tubercular elevations, produced, as sections show, by slender filiform processes of the mesogloea. No special sphincter muscle is present, a circumstance which distinguishes the genus from *Ophiiodiscus*, as already noted, but the general circular musculature of the column wall is fairly well developed, the mesogloea being raised into short unbranched processes which support it. The ectoderm consists principally of glandular cells, and measures about 0.817 mm. in thickness; the mesogloea is thin, averaging only 0.04 mm. in thickness, though it varies somewhat; while the endoderm, containing numerous "yellow cells," is about 0.065 mm. in thickness.

The disc is flat, and transverse sections show a fairly well-developed muscular layer, entirely ectodermal, however; that is to say, it is arranged on elevations of the external surface of the mesogloea, and is not at all imbedded within its substance as in *Ophiiodiscus*. The gonidial angles of the mouth are very distinct. The tentacles are marginal, simple, and cylindrical, hanging down over the column as in *Ophiiodiscus*. They are long, measuring about 3 cm. in length, and are arranged in several cycles, their formula being apparently 6, 6, 12, 24, 48, 96 (?). In structure they resemble closely the disc, there being a well-defined nerve layer (Pl. III., Fig. 13). The difference in the structure of the inner and outer surfaces of the basal portion of the tentacles which Hertwig describes in *Ophiiodiscus* does not obtain here, although their marginal situation does entail some peculiarities. Thus, immediately at the base in some of the tentacles an endodermal musculature can be perceived as well as an ectodermal, which latter again is frequently

absent on one surface. The endodermal musculature is evidently a continuation upwards of that of the column wall, but it soon disappears, and a very short distance above the base the tentacles throughout their whole circumference resemble the disc.

The pseudo-tentacles are six in number, and not five, as Duchassaing and Michelotti ('60) describe, one having evidently been overlooked by them, or else they chanced upon an abnormal specimen. In both of the specimens obtained at New Providence six were present, and there can be no doubt but that this is the normal number. They alternate with the six primary tentacles. Each has a somewhat elongated stout basal portion, which measures 3.8 cm. in length by 0.8 cm. in diameter. This divides into two equal stems (Pl. III., Fig. 11), which again dichotomize many times until a dendritic structure is produced, which projects some distance beyond the decurved tentacles. In structure the pseudo-tentacles are somewhat peculiar. Transverse sections through the basal portion (Pl. III., Fig. 12) show the ectoderm to be identical in composition with that of the column, and the ectodermal surface of the mesogloea is raised into fine processes as in the column-wall. The musculature of the endoderm is, however, very characteristic, bands of muscle cells (*m*) being arranged at intervals around the circumference, the surface in the portions intervening between the bands being destitute of muscle cells. A nervous layer can be traced all the way round, but is only well developed over the bands, being in the intervals exceedingly delicate and sometimes scarcely discernible. In the finer branches this arrangement of the endodermal muscles becomes much less distinct, and finally disappears altogether. In the terminal branches the ectoderm is markedly changed in structure, becoming densely loaded with nematocysts, while elsewhere, as in the column, these are absent. It may be remarked here that this is the only anemone of all those I examined and handled which stung at all severely, though this may in part be due to the pseudo-tentacles having come in contact with the more delicate skin between the fingers. Probably in the same circumstances the stinging powers of *Disco-soma* would have been quite as marked.

I was unable to ascertain the number of the mesenteries, but they are quite numerous, a pair probably corresponding to each tentacle. Half of the pairs are decidedly larger than the others,



the long and the short pairs alternating, the former only being perfect. The mesogloea is exceedingly delicate. Longitudinal muscles, moderately strong (Pl. III., Fig. 14), are developed on all the mesenteries, as well as a very weak parieto-basilar. All (including the directives?) are gonophoric. The specimen examined was a female, and the number of ova present seemed very great. From this description it will be seen that the arrangement of the mesenteries is very different from what occurs in *Ophiodiscus*, in which the first three cycles, two of which are perfect, alone possess longitudinal muscles and are not gonophoric, the reproductive organs being limited to the non-muscular mesenteries of the fourth cycle. These differences, taken with others which have already been pointed out, seem to justify a separation of the two genera into distinct families; but, as already remarked, such a separation is as yet hardly necessary.

#### Sub-tribe STICHODACTYLINÆ

= Family Stichodactylinæ, Andres, 1883.

Hexactiniæ, in which some of the interseptal spaces communicate with more than one tentacle, the latter being thus arranged in radial series encroaching upon the central portion of the disc. The tentacles are in some cases all of one form, *i.e.* tentacular, and in other cases are of two forms, some being tentacular and some frondose or of varying form. Base adherent.

#### Family Discosomidæ.

*Synon.* — Discostominæ — Verrill, 1868.

Discosomidæ (pars) — Klunzinger, 1877.

Discosomidæ — Andres, 1883.

Stichodactylinæ, with tentacles of only one form, short and tentacular, and covering the greater portion of the surface of the disc. Sphincter muscle strong and circumscribed.

This family as here limited agrees with Andres' sub-family of the same title. The term employed by Verrill owes its origin to the proposed change of the name of the principal genus *Discosoma*.

## Genus DISCOSOMA, Leuck.

- Synon.* — Priapus (pars) — Forskål, 1775.  
Actinia (pars) — Ellis, 1767.  
Hydra (pars) — Gmelin, 1788.  
Discosoma — Leuckart, 1828.  
Actinodiscus — Blainville, 1830.  
Discostoma — Ehrenberg, 1834.

Discosomidæ, with the column either smooth or furnished with verrucæ towards its upper portion. Tentacles rather small and finger-shaped, covering the greater portion of the disc. Sphincter muscle strong, and of the circumscribed variety.

The earlier names under which the members of this genus were included do not call for comment. Ehrenberg ('34) altered the term bestowed by Leuckart, considering it inappropriate; and Verrill adopted this altered name ('68) on the ground that the term Discosoma had been applied to an Arachnid and Discosomus to a reptile by Oken. In retaining Leuckart's original name I have followed Andres, since, as he points out, its application to the Actinian has the priority, the Arachnid not having been named till 1830.

7. *Discosoma anemone* (Ellis), Duch. (Pl. I., Fig. 8; Pl. III., Figs. 15-16; Pl. IV., Fig. 1.)

- Synon.* — Actinia anemone, n. sp. — Ellis, 1767.  
Hydra anemone — Gmelin, 1788.  
Discosoma anemone — Duchassaing, 1850.  
Actinia helianthus, n. sp. — Ellis, 1767.  
Hydra helianthus — Gmelin, 1788.  
Discosoma helianthus — Milne-Edwards, 1857.

I have included under the name *Discosoma anemone* both forms described by Ellis, believing that the differences between the two forms indicated by that author were simply due to different degrees of contraction or to age.

This species is very common in the neighborhood of New Providence, especially near the quarantine station on Athol Island, and also occurs at Abaco Island of the Little Bahama reef. It is found along the sandy shores lying buried in the sand, with the tentacle-covered disc exposed, sometimes attached below to loose stones or buried sticks, but more frequently is unattached.

Duchassaing and Michelotti have described it ('60-'66) from Guadeloupe and St. Thomas.

In color (Pl. I., Fig. 8) the column is cream-white shading off above into a brown, occasionally dark seal-brown. The disc is brown, with opaque white patches. The tentacles are greenish brown or white, those of each color being arranged in groups, so that the surface of the animal has a variegated appearance. According to Duchassaing and Michelotti ('60) the color of the tentacles changes so that in the space of some hours they can pass from one color to the other, but I did not observe this peculiarity. The gonidia are well marked, being of a canary-yellow color, while the stomodæum is white.

The base is usually somewhat smaller than the column, and is frequently very irregular in shape. It is capable of adhering firmly to various objects, but not infrequently I gathered specimens which did not seem to be attached to any solid body, but simply imbedded in the sand. The column is capable of considerable extension, but in their normal condition most specimens are more or less contracted, measuring about 1.5-2, occasionally 5 cm. in height. In an aquarium, however, where there was no sand in which the animals might imbed themselves they extended much more, one form measuring in such conditions 13.5 cm. in height. The upper portion of the column is provided with verrucæ arranged in vertical series, which are, however, in many cases very indistinct, being of the same color as the column. In some specimens, on the other hand, they stand out very prominently, being of a brownish or greenish brown color. In structure these verrucæ resemble closely those of *Aulactinia*, being characterized by the absence of the large club-shaped glandular cells which are elsewhere present in the ectoderm of the column. The layer of small pyriform cells, so evident in *Phymanthus* (*q. v.*), was not clearly distinguishable in sections, though there were apparently numerous peculiar cell elements in that region of the verrucal epithelium in which the pyriform cells occur in *Phymanthus*.

An exceedingly well-developed circumscribed endodermal sphincter muscle (Pl. III., Fig. 15) is present, notwithstanding that the animals do not seem to be able to retract the tentacles; in *Polysiphonia tuberosa*, in which there is a mesoglæal sphincter muscle, R. Hertwig ('82) observed the same absence of a



retraction of the tentacles by the folding in of the upper part of the column over them. In transverse sections the sphincter muscle of *Discosoma* is oval and attached to the column wall by a distinct pedicle, the mesogloea of which breaks up quickly into a number of processes, although towards the inner side a prolongation of it, much reduced in size, is continued on towards the extremity of the swelling, processes arising from it in a somewhat pinnate manner. A little below the point of attachment of the pedicle to the column wall are a series of well-marked muscle processes, succeeding which comes a short interval in which all such processes are wanting; below this they again make their appearance, being now relatively small, however, and extend the rest of the way down the column.

The ectoderm of the column is raised into slight elevations (Pl. III., Fig. 16), not sufficiently large, however, to be plainly noticeable to the naked eye, or to give a tuberculate appearance to the column. They are produced by solid conical elevations of the mesogloea, and are very numerous and closely packed, the ectoderm covering them being quite undifferentiated and resembling in structure that which covers the walls in the intervals between them. The endoderm cells throughout contain numerous "yellow cells."

The tentacles are short finger-like processes, and are very numerous in the larger specimens, their number approaching in some cases 600. All the tentacles of each radial series communicate with the same intraseptal space, but the number in each series is subject to considerable variation, and I was not able to discover any law regulating this number. Some of the series were very evidently longer than the others, extending nearly to the mouth, but the length of these rows varied, as also did the number of shorter rows between successive longer ones, there being in some cases only two or three, in other cases five or six. I endeavored by carefully dissecting away in succession the mesenterial pairs, and the tentacles communicating with their intra-mesenterial spaces, to determine the relation between the number of tentacles, and the grade of the septum; but the process was one of considerable difficulty, and, so far as I carried it, yielded no definite results. In structure the tentacles resemble closely those found in members of the sub-tribe Actininae. The ectoderm was exceedingly richly supplied with nematocysts,

which perhaps give rise to the peculiar clinging power possessed by the tentacles in fresh specimens. They adhere to the fingers quite firmly when handled, and a quite decided effort is required to detach them. I believe this to be due to the numerous nematocysts, as I discovered no glandular or suctorial structures in the tentacles. No sensation of stinging was observed, however, but this does not necessarily follow the penetration of the hard skin of the hands by the threads of the nematocysts. In the lower layer of the ectoderm is a delicate nervous layer. The ectodermal musculature is longitudinal, and is by no means strong, the mesogloæal processes being quite low. On the endodermal side of the mesogloæa are circular muscles, and the endoderm cells contain numerous "yellow cells." In longitudinal sections a fibrillar layer containing some nuclei could be observed, separated from the mesogloæa by the muscle cells; it is evidently the endodermal nerve-layer, similar to that which the Hertwigs have described ('79) in *Tealia crassicornis*. It is most clearly seen just where the tentacles join the disc, becoming rapidly indistinct towards the apex of the tentacles, so that in that region it is impossible from my preparations to assert its presence.

The small portion of the disc left uncovered by the tentacles is smooth, and structurally presents no peculiar characters, the musculature, like that of the tentacles, being weak. The mouth is large, with well-marked gonidial folds.

The mesenteries are very numerous, varying, according to the size of the individual, from 100 to 200 pairs, which are alternately perfect and imperfect. The longitudinal and parietobasilar muscles are not particularly strong, the former being limited to the outer portion and having the processes arranged in a characteristic manner. A series of elevations of the mesogloæa give rise to a number of radiating processes, which branch to a slight extent, there being a few short and stout processes in the intervals (Pl. IV., Fig. 1). The nearest approach to such an arrangement that I am aware of has been described by R. Hertwig in *Polystomidium patens*. The inner mesenterial stomata are present, and are comparatively large; there is no trace of the external stomata. The specimens examined were females, and the reproductive organs were present on all the mesenteries, with the exception probably of the directives. My

preparations were not, however, quite satisfactory for the determination of the relation of the gonophoric and sterile mesenteries. A filamental apparatus is present.

Several specimens were obtained in various stages of division, and there can be no doubt but that this species must be added to the list of those which are known to reproduce non-sexually in this manner.

The form described by Ehrenberg ('34), Klunzinger ('77), and others, from the Red Sea, occurring also at Mozambique, and known as *Discosoma giganteum* (Forsk.), is very close to the one here described, if one can judge by the descriptions which have been given of it; but differs somewhat in size, measuring 10 cm. in height. It must, however, be considered a distinct species until a further study of it has been made. It is worthy of note that Forskal mentions the adhesiveness of the tentacles of *D. giganteum*, which, as above stated, is very noticeable in *D. anemone*.

Mosely, who first described the deep-sea forms *Corallimorphus*, considered them most closely allied to *Discosoma*. R. Hertwig ('82), however, established a separate family for the genus while recognizing the probability of a close similarity in structure to *Discosoma*, but placing importance upon the nature of the tentacles, which are of the knobbed variety and arranged in an inner and an outer cycle, a tentacle of the former occurring on the same intraseptal space with one of the latter cycle. He also suggested a similarity to the *Corynactidæ*, which likewise possess knobbed tentacles. It is evident, from the description given above of *Discosoma*, that *Corallimorphus* cannot be placed in the same family with it. The presence of the strong circumscribed muscle in the former genus at once distinguishes it, there being no special circular muscle at all in the latter. A study of *Corynactis* is required to ascertain its nature in this respect.

#### Family RHODACTIDÆ, Andres.

*Synon.* — Phyllactininae (pars) — Klunzinger, 1877.  
Rhodactidæ — Andres, 1883.

Stichodactylinae with tentacles of two kinds. The margin is furnished with tentacles of the ordinary kind arranged appar-



ently in a simple cycle, while upon the surface of the disc, and separated from the marginal tentacles by a naked space, are numerous tuberculiform or lobed tentacles, arranged more or less radially. No sphincter muscle, the musculature throughout being very weak.

I have thought it proper to extend this family somewhat, so as to include it in a genus referred by Andres to the family Crambactidæ. My reasons for so doing will be given when discussing the genus.

Genus RHODACTIS, Milne-Edwards.

*Synon.* — Metridium (pars) — Ehrenberg, 1834.  
Actinaria (pars) — Deshayes, 1837.  
Rhodactis — Milne-Edwards, 1857.

Rhodactidæ with smooth column. Marginal tentacles very short and conical; disc tentacles more or less lobed, arranged in two groups, one, consisting of the greater number of tentacles, towards the periphery of the disc, and the other separated from the peripheral group by a naked space, and consisting of a few tentacles only, situated around the mouth, and therefore labial.

8. *Rhodactis Sancti Thomæ* (Duch. and Mich.). (Pl. I., Fig. 9; Pl. IV., Figs. 2, 3.)

*Synon.* — Actinotryx Sancti-Thomæ — Duchassaing and Michelotti, 1860.  
Actinothrix Sancti-Thomæ — Andres, 1883.

This form, first described by Duchassaing and Michelotti ('60), is made by them the type of a new genus. They, however, recognized its similarity to *Rhodactis*, the distinction being that "les appendices, qui avoisinent la bouche, sont simples et bilobés, tandis que la disposition des tentacules placés entre les couronnes interne et externe est aussi différents." Andres, however, considers this statement "quasi inintelligibile," and believes that the species has nothing to do with *Rhodactis*, and places it, along with the genus *Crambactis*, in another family. After having studied this so-called *Actinothrix*, I have come to the conclusion that it is a *Rhodactis*, the difference between it and *Rhodactis rhodostoma* being of specific and not of generic importance.

*Rhodactis Sancti Thomæ* is not uncommon at New Providence, occurring firmly attached to the coral rock in shallow water. It

is exceedingly difficult to detach it without injury, and when irritated secretes an enormous amount of mucus, its separation from the rock being thereby rendered more difficult. In color (Pl. I., Fig. 9) the column is of a brownish purple, frequently with a more or less greenish tinge; the disc is similar in color, with green bands radiating from the raised peristome towards the margin; the peripheral tentacles are pale bluish green, with brown tips, the disc tentacles being seal-brown or a somewhat lighter shade of the same color; the mouth and œsophagus are white.

This form is known from St. Thomas, where it was originally discovered. Some of the specimens obtained at New Providence are sufficiently light colored as to agree fairly well with the description given by Duchassaing and Michelotti of the St. Thomas examples.

The column measures about 1.6 cm. in height, and is smooth. It expands considerably above, the margin being frequently, in full expansion, folded back so as to conceal the column. No special sphincter muscle is present, and in fact the circular muscles of the column are throughout exceeding feebly developed, a fact which agrees with the small power of infolding the disc which these forms possess; in a single instance only did I meet with an individual which had this power. The ectoderm of the column is thrown into longitudinal series of minute elevations, each series corresponding with an interval between two mesenteries, and the elevations being formed by delicate processes of the rather thin mesogloea ( $0.85\ \mu$ ). So far as could be ascertained there is a complete absence of cnidoblasts in the ectoderm, the only cells present being apparently glandular, the contents of which do not stain, sections through the column wall having thus a very characteristic appearance. The endoderm also contains gland cells, and is richly packed with "yellow cells."

The margin is occupied by the single row of peripheral tentacles, which are short, cylindrical, and abruptly acuminate. They vary somewhat in size, a small one usually alternating with a larger one, though frequently two or three small ones will intervene between two succeeding large ones. The number of these tentacles varies; in larger specimens they are somewhere in the neighborhood of 150.

The disc is covered for the most part with short, stout tentacles, whose surface is elevated into a varying number of tuberculiform or short, finger-like processes. They are arranged somewhat irregularly, and are situated principally midway between the margin and the mouth, a circle of them, however, surrounding the mouth, being separated by a considerable naked space from the rest. The portion of the disc adjacent to the margin is also naked. There is no trace at the bases of the tentacles of any such depressions with elevated margins as occur in *Rh. rhodostoma*, but this must be regarded as a specific distinction only, and not generic. The histological structure of the disc, marginal tentacles, and disc tentacles are similar throughout. The ectoderm (Pl. IV., Fig. 2, *ec'*) is thin, measuring in a disc tentacle, somewhat contracted,  $34\ \mu$ , on the disc near the margin when expanded,  $27.2\ \mu$ . A peculiar feature of the ectoderm throughout is the entire absence of nematocysts, there being on the other hand numerous gland cells. The muscular layer is exceedingly delicate, a single row of muscle cells lining the smooth external surface of the mesogloea. The mesogloea, like the ectoderm, is very thin, measuring, in the disc tentacles,  $10.2$  to  $13.6\ \mu$ , and in the disc,  $3.4\ \mu$ . The endoderm, however, presents a most remarkable appearance, differing from that of any Actinian I have yet studied. Its general characters are well shown in Pl. IV., Fig. 2, *en'*. It consists of high glandular cells, measuring from  $0.136$  to  $0.17\ \text{mm.}$ , and filled with a clear substance which does not stain, the cell walls and much compressed nuclei standing out very clearly. The cavity of the tentacles is filled with the secretion of these cells, which is apparently a perfectly homogeneous coagulable fluid. Numerous "yellow cells" are imbedded in the contents of the cells, especially towards their proximal ends.

The mouth is large and almost circular, and is elevated considerably above the surface of the disc. The stomodæum is raised into strong folds, as may be seen from Pl. IV., Fig. 3. The gonidia are not at all well marked; in fact, it is not possible to distinguish them.

The mesenteries, like the other regions of the body, have the muscular layers very weakly developed, the longitudinal foldings of the mesogloea, so characteristic in other species, being almost undeveloped and represented only by very slight



rounded elevations. The arrangement of the mesenteries I was not able to make out satisfactorily. The majority of them are perfect, the imperfect ones being usually quite small and appearing to have no regular arrangement. Thus there would be several perfect pairs in succession, followed by one or two imperfect pairs, alternating with perfect ones, and then several more perfect pairs, and so on. It would seem that normally all the mesenteries are perfect, but that a few, for some cause or other, remain undeveloped. All the mesenteries are situated at equal distances, so that the intra- and inter-mesenterial spaces are about equal in width. It is difficult, owing to this and to the very slight development of the longitudinal muscles, to orient the pairs properly, but there are probably two pairs of directives, as in other forms, although I was able to make out with certainty only one of them. R. Hertwig ('82) has described a species in which this is the normal relation, and has founded upon it the tribe Monaulææ. In its general character, however, *Rhodactis* differs greatly from *Scytophorus*, the only genus at present known to belong to the tribe, and on the other hand resembles forms which possess the two pairs of directives, so that I believe that it possesses the second pair, and that its apparent absence in the specimens examined was due to the unsatisfactory nature of the preparations which I studied. The number of the mesenteries is comparatively large; in a small specimen I counted 48 pairs, and in another 52; but in a larger one, judging from the number of the series of ectodermal elevations, there must be in the neighborhood of 150.

The endoderm of the mesenteries is of the same nature as that of the disc, and requires no further description. Imbedded in it were found in the specimens examined numerous cysts, measuring about  $68\mu$  in length by  $27\mu$  in breadth, which looked almost like encysted nematode parasites, the comparative rarity of their occurrence lending somewhat to the illusion. Careful study, with high magnification, showed them to be large nematocysts. The thread contained in the interior is not very long, and is finely and obliquely striated. Occasionally considerable numbers of these bodies occur together, apparently more especially in the mesenterial filaments, but their number taken altogether is comparatively small. They were present in the endoderm of the disc (Pl. IV., Fig. 2, *ne*) as well as in that of the

mesenteries, and were, so far as I could discover, the only nematocysts present.

None of the specimens examined showed any traces of reproductive organs. The spawning season was probably just over, as I obtained a few free-swimming larvæ from a vessel in which a couple of this species were kept over night.

#### Genus *HETERANTHUS*, Klunz.

*Synon.* — *Ricordea* — Duchassaing and Michelotti, 1860.

*Heteranthus* — Klunzinger, 1877.

*Actinothrix* — Andres, 1883.

*Rhodactidæ*, with short marginal tentacles, forming a single row, and with the disc covered with tuberculiform tentacles arranged radially.

The type species of this genus is *Heteranthus verruculatus* of Klunzinger ('77), which has the characters given above. Certain features presented by it are not, however, met with in the Bahaman species; for instance, the verrucæ of the column are absent in the latter form, as are also the bunches of tubercles on the margin. These may be looked upon, however, as specific differences, and Klunzinger's definition has consequently been altered. Andres ('83) associated *H. verruculatus* with the *Actinotryx Sancti Thomæ* of Duchassaing and Michelotti, retaining that generic title inasmuch as it was the older. I have stated my belief that *Actinotryx* is really a *Rhodactis*, and consequently that term should be disregarded, and the one employed by Klunzinger retained.

I have also departed from Andres' arrangement in placing *Heteranthus* in the family *Rhodactidæ*. That author associates it with *Crambactis* in the family *Crambactidæ*. The tubercular disc tentacles in *Heteranthus*, however, are much more similar to the lobed ones of *Rhodactis* than to the foliose ones of *Crambactis*, and furthermore, the marginal tentacles of *Heteranthus* and *Rhodactis* are in a single row, while those of *Crambactis* are arranged in several cycles. Consequently I associate the two former genera together in one family, leaving *Crambactis* as the sole genus of another.

The term *Ricordea*, proposed by Duchassaing and Michelotti ('60) as a new genus for the reception of the species to be de-

scribed below, has the priority over Klunzinger's term; but, since the characters which were assigned to it by its authors are, if anything, specific and not generic, I have ventured to disregard its priority. The justice of this is no doubt open to question, but in this case I think that such a substitution has much in its favor. Not only does Klunzinger's definition characterize the genus, which cannot be said of Duchassaing and Michelotti's, but the term *Heteranthus* itself is preferable as indicating a character of the forms to which it is applied, and is much more in harmony with Actinian nomenclature. The characters assigned to *Ricordea* will be discussed below in connection with the description of the species.

9. *Heteranthus floridus* (Duch. and Mich.). (Pl. I., Fig. 10; Pl. IV., Figs. 4-5.)

*Synon.* — *Ricordea florida* — Duchassaing and Michelotti, 1860.

This form occurs not unfrequently adhering to stones in shallow water, and was usually found in association with *Rh. Sancti Thomæ*. Like that species it adheres very firmly to the surface of the rocks, so that it is exceedingly difficult to detach it without injury, especially since when touched it throws off large quantities of mucus.

In color (Pl. I., Fig. 10) it is pale flesh color below, shading off above into a purplish brown. The disc and peristome are also of a purplish brown, with a very decided green tinge. The outer tentacles are green, and the disc tentacles of the same color as the disc. The mouth and stomodæum are white.

The base, on account of its firm adhesion to the rock and its accommodating itself to the uneven surface of attachment, is usually very irregular and folded so as to project into the cavity of the body, and it retains these foldings to a greater or less extent when removed from the rock. This circumstance, together with the small height of the specimens, rendered it very difficult to obtain preparations from which the arrangement of the mesenteries, etc., could be accurately determined.

The column is low, measuring in height 0.45 cm., and in diameter about 1.2 cm. Its outer surface is raised into minute tubercles hardly visible to the naked eye, and supported by exceedingly delicate, frequently somewhat branched, processes



of the thin mesoglœa (Pl. IV., Fig. 4). I never observed these tubercles to be capable of causing the adhesion of particles of sand, etc., although the ectodermal cells covering them seem to be somewhat different from those in the intervals, being more delicate, resembling somewhat those characteristic of verrucæ. The surface of the elevation is not depressed as in verrucæ, and they differ in this respect from these of *H. verruculatus*, which Klunzinger describes as being provided with verrucæ situated especially towards the upper part, but often extending almost to the base. The ectodermal cells are delicate, but present no remarkable characteristics. The endoderm contains numerous gland cells, and is richly provided with "yellow cells." The muscular layer throughout is very weak, and there is no trace of a sphincter muscle, unless two or three processes of the mesoglœa, widely separated, and similar to those which support the ectodermal tubercles, may be considered as representing it.

The margin bears a number of short conical tentacles similar to those of *Rhodactis*. No bunches of tubercles are to be observed similar to those of *H. verruculatus*. The disc, which measures 1.3 cm. in diameter, is covered towards the periphery with rows of short tuberculiform tentacles arranged radially. There is considerable irregularity in the length of the various rows; their number is about 36, though it is difficult from my specimens to give an exact number. In structure these tentacles are characterized by the small development of the muscular layer, by the total absence of nematocysts as in *Rhodactis*, and especially by the nature of the ectoderm cells of the apex (Pl. IV., Fig. 5). Over the general surface they present no peculiarities, but just at the apex, where in preserved specimens there is a translucent circular spot, the cells become exceedingly delicate and closely packed together, so as to resemble very closely in general appearance what has been previously described for the verrucæ of *Aulactinia*. The mesoglœa of the tentacles and disc, like that elsewhere in the body, is very thin. The central portion of the disc is bare, and from it the peristome rises up somewhat abruptly, so that the mouth is some distance above the surface of the disc. The mouth is almost circular, and the gonidial angles cannot be distinguished. The walls of the stomodæum are raised into folds as in *Rhodactis*.

I was not able to make out in this form the arrangement of the mesenteries. The longitudinal and parieto-basilar muscles are as slightly developed as in *Rhodactis*, and, as in that form, the inter- and intra-mesenterial spaces are about equal in width, I counted about 28 pairs of mesenteries in a fair-sized specimen; of these 12 were perfect and the rest imperfect, the latter usually but not always alternating with the perfect ones. I could not distinguish with certainty the directives. None of the specimens examined possessed reproductive organs. The endoderm cells of the mesenteries, though mostly glandular, were by no means so markedly so as in *Rhodactis*, nor did I observe any of the large nematocysts characteristic of that form.

This species I observed in the process of fission. In one specimen the process was nearly completed, the two individuals being quite distinguishable, and united to each other throughout an extent equal to about half the diameter. In another case, however, the process had not extended nearly so far, the only evidence of the fission being the presence of two distinct peristomal elevations, each with a mouth, upon the disc, and a crowding of the rows of disc tentacles on the portion of the disc common to the two mouths.

Duchassaing and Michelotti ('60) describe this form under the name of *Ricordea florida*. The genus is defined as consisting of forms which, though simple when young, become composite when their development is complete; *i.e.*, at this stage the animals have five mouths situated at the centre of the disc, which is elsewhere covered with short obtuse tentacles, not completely retractile. In their second paper ('66) they state their belief that the genus presents relations to *Discosoma* on account of the tentacles being non-retractile, and the disc not being able to close completely. The single species, which they describe as being common at St. Thomas, is of a dark green or blue, presenting a variety with reddish tentacles. The figure of it which they give shows that it is identical with that just described, notwithstanding that no notice is taken of the marginal tentacles. The occurrence of several mouths on the disc is certainly a peculiar feature, and one that would, if no other forms having the same arrangement of the tentacles were known, lead one to make it a generic distinction. There can be no doubt, however,

that it is not of such importance. It is produced by the non-completion of the process of division, and the forms might be compared to such corals as *Fungia* or *Manicina*, which, though individual polyps, still possess several mouths. The remarkable thing about it is its general occurrence, since Duchassaing and Michelotti seemed to have found it almost universal, while it was present in several of my specimens.

Although the facts made out concerning the histology of *Rhodactis* and *Heteranthus* are so meagre, yet sufficient has been ascertained to confirm the conclusion as to the similarity of these two forms, which was arrived at from the study of their external characters. Thus they have in common the absence of a circular muscle, the weak musculature of mesenteries, disc, and tentacles, the elevation of the œsophagus wall into a number of very pronounced folds, the excessive proportion of glandular cells in the endoderm, and the very slight development of nematocysts. Taking these points in conjunction with the similarity in the form of the tentacles, the propriety of associating these two genera in the same family is, I think, established.

#### Family Phymanthidæ, Andres.

*Synon.* — Phyllactiniæ (pars) — Klunzinger, 1877.

Phymanthidæ — Andres, 1883.

Stichodactylinæ provided with two kinds of tentacles, marginal ones large, tuberculiferous or pinnate, and discal ones small and papilliform.

It seems a question whether this family should not be fused with that of the Phyllactidæ. Tuberculiferous and foliose tentacles are merely different degrees of the same kind of specialization, and the papilliform discal tentacles are simply very much shortened conical ones. It seems well, however, to leave them separate just now.

#### Genus PHYMANTHUS, M.-Edw.

*Synon.* — Actinia (pars) — Lesueur, 1817.

Actinodendron (pars) — Ehrenberg, 1834.

Phymanthus — Milne-Edwards, 1857.

Phymanthidæ with the column provided with longitudinal rows of verrucæ in its upper part. No sphincter muscle.



10. *Phymanthus crucifer* (Les.), Andres. (Pl. II., Fig. 1; Pl. IV., Figs. 6-11.)

*Synon.*—*Actinia crucifera*—Lesueur, 1817.

*Cereus crucifer* (Actinia)—Duchassaing and Michelotti, 1866.

*Phymanthus cruciferus*—Andres, 1883.

Several specimens of this form were obtained, usually fastened to blocks of coral rock in shallow water.

The column (Pl. II., Fig. 1) is of a cream-white ground color, varying toward pinkish at the base, and extending up from the base are irregular streaks of crimson. The verrucæ are of a rich crimson and are very evident upon the whitish ground. The tentacles are brown, marked with transverse bars of white somewhat elevated above the general surface. The disc is brown, in some specimens covered with irregular blotches of white, and in all cases showed a very marked greenish iridescence when viewed with the light falling on it obliquely.

The base is firmly adherent, and only slightly larger than the column. This varies considerably in length. When fully contracted, the animal is only a couple of centimetres high and conical in shape, the disc being widely expanded, while the column is much contracted towards the base. When expanded, it measures 8.3 cm. in height and 4.75 cm. in diameter. The verrucæ are limited to the upper portion of the column, and are arranged in vertical rows. A transverse section through one of these structures and the adjacent column wall (Pl. IV., Fig. 6) shows a marked difference in the histological structure of the two parts. In the general ectoderm of the column (*ec*) are many club-shaped glandular cells measuring  $6.4\mu$  in diameter, whose contents are exceedingly granular, and also numerous cnidoblasts containing smooth capsules measuring  $16.8\mu$  in length and  $2.4\mu$  in diameter. The ectoderm of the verrucæ (*mec*), on the other hand, is composed of cells which took the staining (Borax Carmine) much more deeply, and gave the appearance of very fine fibrillation to the layer. Towards the mesogloea, but separated from it by a short interval, are numerous bodies of a somewhat oval shape (*py*) which take the staining very deeply. Sections through the verrucæ were macerated for some time in 0.2 per cent acetic acid. The general ectoderm of the column separated very readily from the mesogloea,

but that of the verrucæ remained firmly attached, and could only be separated with difficulty, as in *Aulactinia* and *Heliactis*. When separated, the cells composing it were seen to be exceedingly delicate and very uniform in thickness, being only slightly dilated towards the outer extremity. There were none of the glandular cells or cnidoblasts of the general ectoderm present. The darkly stained bodies seen in the sections were found to be small oval or pyriform structures, measuring  $14.4\mu$  in their longer diameter, and with a maximum thickness of about  $4.8\mu$ . It is possible that they may be glandular, but I was unable to discover that they possessed any connection with the exterior, though some of the more perfectly isolated ones seemed to be broken off at one end, and there may possibly have been a very fine process or duct extending to the surface. There appear to be no nerve cells present in the verrucal epithelium, unless these pyriform bodies be such, and no muscle cells.

Von Heider observed ('77) in his investigation of *Heliactis bellis* (*Sagartia troglodytes*) that the ectoderm of the verrucæ was less readily separable from the mesoglœa than that of the general surface, and also perceived the difference in the shape of the cells which he describes as follows: "Eine solche (Saugwartze) mit Osmium oder Alkohol gehärtet und untersucht (Fig. 38) erweist sich als aus zahlreichen parallelen Stäbchen zusammengesetzt, die spindelförmig und beiderseits ziemlich spitz endend, im Innern fein gekörnt erscheinen und so dicht aneinander gedrängt sind, dass die einzelnen Elemente nur am Rande des Schnittes, wo sie sich isoliren, deutlich zu sehen sind." According to my observations, the spindle-shape was not so universal a characteristic, though some cells presented it. Von Heider did not observe any of the peculiar pyriform cells, and it is possible that they may not be present in the verrucæ of *Heliactis*, though it seems more probable that they were overlooked, as they might very readily be, in *Bunodes tæniatus*, for instance.

With regard to the mode of action of the verrucæ in producing the adherence of foreign bodies, Gosse ('60) was of the opinion that it was a process of suction, agreeing in this with Hollard ('51) and Haime ('54). I do not think this is the case, however. The absence of muscle cells in the verrucal epithelium, and the abrupt discontinuity of the muscle processes at the edge of the verrucæ as seen in sections of *Aulactinia*, are

against it. Von Heider's idea, that it is due to a special secretion produced by the ectodermal cells, seems much more in accordance with the histological structure. I was inclined at first to consider the pyriform cells the producers of the secretion, but am now undecided as to whether they are not really nerve ganglion cells. They occupy the position of the nerve layer of other parts of the body, and their slight development in some species seems to indicate that they are not directly concerned in producing the adherence of foreign bodies. I regret that I was unable to study maceration preparations of fresh specimens, from which, no doubt, this point might be settled; and it would be exceedingly interesting, in connection with the physiology of secretion, to make such observations, and determine the existence or non-existence of nerve cells in the verrucæ.

The mesoglœa of the column wall is rather thick (Pl. IV., Fig. 7), and is raised into numerous obtuse elevations. The endoderm is as usual abundantly supplied with "yellow cells." There is no special sphincter muscle distinct from the ordinary endodermal muscle layer of the column, and, consequently, there is no infolding of the disc in contraction.

The external tentacles are conical, numerous, and entacmæous. They are arranged in five cycles closely crowded together. The innermost cycle consists of 24 tentacles, as does also the next external, the third of 48, the fourth of 96, and the fifth of 192; the third and fourth cycles being much crowded together, so as to look like one. Upon the inner faces of each of the tentacles are three or four transverse ridges which dilate into tubercles at either extremity, and are due, as sections show (Pl. IV., Fig. 8) to an increased thickness of the mesoglœa in these regions. Lesueur ('17), in his brief description of this form, notes that "the tranverse tubercles are enlarged at their extremities, sometimes bilobated"; and I observed a tendency towards bilobation in some of my specimens. In Klunzinger's specimen of *P. loligo* ('77) the tentacles are "recht und links von der Mittellinie, mit kleinen rundlichen Warzen besetzt, die oft durch Querwülste jederseits verbunden sind, wodurch sie wie gefiedert sind. Andermal sind sie zu unregelmässigen Läppchen oder Gruppen verbunden wie Ehrenberg zeichnet." The latter forms approach the Bahaman specimens more than those figured



by Klunzinger, and show an intermediate stage in the complication of the mesogloæal enlargements, the Bahaman forms representing the simplest stage; while the form mentioned by Klunzinger in a foot-note, the *P. pinnulatum*, Martens, from Singapore, a specimen of which is in the Berlin Museum, represents the most complicated condition, the pinnulation being even more marked than in Klunzinger's figures.

The tentacles of the disc are small wart-like structures, whose structure is shown in Pl. IV., Fig. 11. Lesueur ('17) describes the tentacles as perforated warts; but I was not able to distinguish any trace of a pore in my sections. The ectodermal muscle layer of the disc is not very strong, the nerve layer (*n*), as in the tentacles, being well marked. The ectoderm is raised into numerous elevations, as may be seen from Fig. 11, *ec*, the mesogloæa not taking part in their formation.

The mesenteries are arranged in four cycles, of which the first consists of 12 mesenteries, which are attached to the stomodæum throughout its full extent; the second, likewise of 12, has them attached only about half-way down the stomodæum; while the third cycle has its 24 mesenteries entirely free and imperfect. The longitudinal and parieto-basilar muscles are present, the former being fairly well developed (Pl. IV., Fig. 9) and limited to the outer two-thirds of the non-reproductive portion of the mesentery; while the latter, its upper margin forming a fold upon the surface of the mesentery, is limited to its lower one-quarter. The inner stomata are present, but I was unable to determine the presence of any outer one.

All the mesenteries, even the directives, are gonophoric, and the animals are bisexual. In connection with the testes I observed what seems to be a structure corresponding to the "filamental organ," which the Hertwigs ('79) have described in ovaries of certain forms examined by them. From their studies of *Adamsia* (*Calliactis*) they were inclined to consider this peculiar organ a portion of the protoplasm of the ovary; but later, R. Hertwig ('82) found in *Corallimorphus rigidus* positive proof of its origin from the endodermal epithelial cells in the neighborhood of the ova. I am not aware that its existence has hitherto been definitely described in connection with the testes, though what Jourdan has described ('77) as occurring in the testes of *Actinia equina* is probably of this nature. Its occur-

rence in *Plymanthus* is consequently interesting. In structure (Pl. IV., Fig. 10) it is essentially similar to what Hertwig has described; *i.e.*, it consists of peculiarly modified endodermal cells which stain deeply, and are consequently very evident in sections. I am unable to say whether the filamental apparatus is present in the ovaries likewise of these forms, since all the specimens examined were males.

This form seems to occur throughout the whole range of the West Indies. Lesueur ('17) observed it at Barbadoes, and Duchassaing and Michelotti at the same island and also at St. Thomas. There can be no doubt as to the identity of the forms described by these authors with that obtained by me in the Bahamas. A figure is given by Duchassaing and Michelotti ('66) which has apparently been overlooked by Andres. It is evidently, however, of a contracted specimen, and cannot be considered a good representation. The animal figured by Ellis ('67) without description, and named *Actinia aster*, has never been sufficiently characterized to permit of identification, although it has been included by many systematic authors in their review of the Actinians. The description given by Solander ('86) is very meagre, and includes no specific characters; and Duchassaing and Michelotti ('60 and '66) simply mention it, without any description. Judging from the figure given by Ellis, it seems possible that it may be identical with *Plymanthus crucifer*; but the uncertainty of such an identification is too great to warrant the insertion of the name among the synonyms given above.

#### Family Phyllactidæ.

*Synon.* — Phyllactinæ (pars) — Verrill, 1868.

Stichodactylinae provided with tentacles of two kinds. The peripheral ones are foliose (fronds), while those towards the centre of the disc are simple and conical.

#### Genus OULACTIS, M.-Edw. and H.

*Synon.* — Actinia (pars) — Lesueur, 1817.

Metridium (pars) — Dana, 1849.

Actinostella — Duchassaing (teste, Andres).

Oulactis — Milne-Edwards and Haime, 1851.

Phyllactidæ with the column provided with longitudinal rows of verrucæ in its upper part. The foliose marginal tentacles (fronds) not arranged in radial series of different degrees of development. No sphincter muscle.

It seems probable that Verrill's genus *Lophactis* ('68) should be included here, leaving only three genera in the family, viz., *Phyllactis*, *Oulactis* and *Asteractis*.

11. *Oulactis flosculifera* (Les.), Duch. and Mich. (Pl. II., Fig. 2; Pl. IV., Figs. 12-14).

*Synon.* — *Actinia flosculifera* — Lesueur, 1817.

*Oulactis flosculifera* — Duchassaing and Michelotti, 1860.

*Oulactis conchilega* — Duchassaing and Michelotti, 1860.

*Oulactis foliosa* — Andres, 1883.

Andres ('83) considered the identification of this form by Duchassaing and Michelotti with Lesueur's *Actinia flosculifera* to be erroneous, imagining the form described by the last-named author to be more probably an *Evactis*. It seems, however, that Lesueur's description, though not as clear as is desirable, agrees fairly well with this form, his marginal "rows of tubercles surrounded with small warts" being a poor description of the external fronds. The term *O. conchilega* is the name given in the index to the plate of Duchassaing and Michelotti's paper to Fig. 7 of Plate VII., which in the text is referred to as *O. flosculifera*.

I obtained a single specimen only of this form, buried in sand up to the tentacles on the shore of the island of New Providence. It has been found also at Green Turtle Cay, Abaco Island, and Lesueur's specimens were obtained at St. Thomas, where it is found not only in sand, but also in the crevices of the rocks.

In my specimen (Pl. II., Fig. 2) the column was of a delicate orange-yellow below, shading off above into cream-white, the verrucæ of the upper part being pure white, and the insertions of the mesenteries showing through as white lines. The fronds were brown and the tentacles clear translucent white, with some opaque white spots, elongated transversely on their inner surfaces. Uthoff's drawings of the specimens seen at Green Turtle Cay represent a somewhat different coloration. They are much lighter, the column being translucent white with only a very faint yellowish tinge, the insertions of the mesenteries



showing through, and instead of becoming paler above it darkens rapidly, and in the region of the verrucae is a very decided brown. The fronds are yellowish white, and thus very different from those of the New Providence form, whereas the inner tentacles are of the same color as in that specimen. The description of the coloration which Lesueur ('17) gives agrees with that of my specimen. It is as follows: the "margin and centre of the disc and tubercles (*i.e.* fronds) of an umber color, tentacula of the same color but paler, furnished with several oblong white spots, with a blackish brown point in the centre of each spot." On the other hand, Duchassaing and Michelotti's specimens ('60) are apparently markedly different from any of the others. I quote their description, so far as it refers to the coloration, verbatim: "Le corps a une couleur verte disposée en lignes ou zones longitudinales." "Le disque est verdâtre; les tentacules d'un jaune clair."

I do not think it necessary to consider these various forms distinct species, but prefer to group them together as color varieties, three such being distinguishable. The predominating colors of these are:

*Var. a.* White, becoming darker above, fronds yellowish white.

*Var. β.* Yellow, fronds brown.

*Var. γ.* Greenish.

The size and shape of the column varies considerably, according to the amount of expansion. When moderately expanded (Pl. II., Fig. 2) it is cylindrical, and measures 8.9 cm. in height and 4.4 cm. in diameter; but when fully expanded, becomes much flatter and broader, assuming the form represented in Pl. VII., Fig. 7, of Duchassaing and Michelotti's paper ('60). It is marked with longitudinal inceptions, and towards the upper part is furnished with several longitudinal rows of verrucae, to which particles of shells, sand, etc., adhere. There is no special sphincter muscle, the transverse musculature of the column, although fairly well developed below, becoming obsolete above. Consequently the tentacles are not infolded in contraction. The mesogloea of the column is raised on its outer surface into numerous irregular elevations (Pl. IV., Fig. 12), throwing the ectoderm into numerous folds. The endoderm is comparatively thin, and contains numerous "yellow cells."

The fronds, situated on the periphery of the disc, are in a single cycle, one surmounting each longitudinal row of verrucæ, there being altogether apparently 24, corresponding thus to the intramesenterial spaces. In structure they are irregularly lobed thickenings of the disc, the mesogloea being thrown into numerous folds, and here and there thickened so as to form slight wart-like prominences. They lack the folded muscular layer which is to be found in the disc and in the inner tentacles. These are situated near the mouth, a naked area of the disc being left between them and the fronds. I am not quite certain as to the number of these inner tentacles; I counted 42, but probably the number should be 48, one corresponding to each intermesenterial, and one to each intramesenterial space, or else two to each intramesenterial space, their arrangement not having been made out. They are cylindrical in shape, tapering towards the extremity. Their longitudinal musculature is strong (Pl. IV., Fig. 13, *mp*), the mesogloea being thrown into numerous ridges, over which the muscle cells are arranged.

The disc is structurally like the inner tentacles. The mouth I could not see, the tentacles completely covering it, but presumably the gonidial angles are well marked. In transverse sections through the stomodæum the two gonidial folds are well seen. They extend downwards for some distance, forming two strong languettes (Pl. IV., Fig. 14). Their structure differs noticeably from that of the rest of the stomodæum, the mesogloea being much thickened, the ectoderm much higher than elsewhere, and the nerve layer very distinct. They approach much nearer the column wall than the stomodæum elsewhere does, the gonidial groove being very deep.

The pairs of mesenteries are 24 in number, and probably represent three cycles, the formula for which is 6, 6, 12. All are perfect. Owing to the depth of the gonidial groove the directives are much shorter than the other mesenteries. In all the muscular layers are exceedingly well developed. The inner mesenterial stomata are present, and the mesenteries of the third cycle only appear to be gonophoric. The specimens examined had only male organs.

## Tribe EDWARDSIÆ.

"Actiniaria with eight septa; among which are two pairs of directive septa, whilst the remaining four septa are not paired; all the septa furnished with reproductive organs; tentacles simple, usually more numerous than the septa." (R. Hertwig '82.)

I was not successful in obtaining any forms belonging to this tribe, though they undoubtedly occur in the Bahamas. Dr. H. V. Wilson informed me that during his stay at New Providence, which terminated at the time of my arrival, he obtained several young *Edwardsias* in the tow-net. This method of collecting I did not follow very systematically, and amongst the material brought in found no *Edwardsiæ*.

## Tribe ZOANTHÆ.

Actiniaria provided with paired mesenteries, each pair consisting of a large perfect macroseptum and a small imperfect microseptum, except in the cases of the two pairs of directives, one of which, the dorsal, consists of two microsepta, and the other, or ventral, of two macrosepta. In some forms the second pair of septa from the micro-directives on each side consists of two macrosepta. Each pair is provided with transverse muscles on the faces turned toward each other, except the directives, in which the muscles are on the faces turned from each other. The increase in the number of the mesenteries takes place by the formation of new pairs in the interspace on either side of the ventral directives.

## Family Zoanthidæ.

Zoanthæa, in which the individual polyps are usually united into colonies; the various individuals being either connected by stolon-like canals or by a common expansion (cœenchyma), with the endodermal cavities of which the cavities of the polyps unite.

Cuvier ('98) was the first to separate the Zoanthids from the other Actinians, defining the group as consisting of forms "qui ont la bouche et les tentacules comme les Actinies, mais dont le



corps est plus grêle par en bas que par en haut ; ce qui leur donne absolument l'air d'une fleur portée sur un pédicule." He places in the group *Actinoloba dianthus* and *Z. sociata*, the latter of which only belongs to the group as now limited. Later, Cuvier ('17) made the formation of colonies the characteristic feature of the group. Ehrenberg ('34) established a definite family for the group, naming it Zoanthinæ and making it equivalent to all the other forms which constituted the family Actininiæ. This arrangement was retained by various authors ; Gosse, however ('60), separated the Actinaria, with which he associated the corals, into four tribes, viz. : Astræacea, Caryophyllacea, Madreporacea and Antipathacea. The first of these contained the majority of the Actinians, the Zoanthidæ and Capneæ, however, being relegated to the second group, which also contained the Turbinolidæ, Oculinidæ, and some other families of corals.

In 1867 Gray ('67) divided the Zoanthinæ into two sub-groups, separating from the fleshy forms those with incrustations of foreign material, forming of the latter the sub-group *Zoanthini palythæinæ*. Verrill ('68) recognized the necessity for a more perfect subdivision of the Zoanthids, and raised the group to the dignity of a sub-order, the Zoanthaceæ, still equivalent, however, to the rest of the Actinians, and including the families Zoanthidæ, Bergidæ, and Orinidæ, holding doubtful the propriety of establishing a fourth family for the separate attached forms which had been described under the generic name *Isaura*, (Savigny) and *Hughea* (Lamouroux.) *Sphenopus* he considered related to the Edwardsians, and hence did not take it into consideration. Verrill's arrangement marks an epoch in the classification of the Zoanthids, his families Zoanthidæ and Bergidæ being equivalent to the same groups as now defined, although the Orinidæ (which includes a single species of *Orinia* described by Duchassaing and Michelotti ('60)) probably does not belong to the sub-order at all, but contains a form related perhaps to some of the deep-sea forms, with pores instead of tentacles, which were obtained by the "Challenger."

Klunzinger's arrangement, so far as it goes, does not present any advance on Verrill's, but Hertwig ('82), having discovered the peculiar arrangement of the mesenteries of Zoanthids, Ceriantheæ and Edwardsiæ, makes of them three tribes, each equivalent to the Hexactiniæ, which includes the majority of the remain-

ing forms. He recognizes two families in the tribe Zoantheæ, the Zoanthidæ and the Sphenopidæ. Andres' classification ('83) is not so advanced as that of Hertwig, since he makes the family Zoanthinæ equivalent to the sub-tribes of the Hexactiniæ as here recognized.

I would recommend an arrangement combining those of Hertwig and Andres. I would recognize Hertwig's tribe Zoantheæ and its equivalency to the Ceriantheæ, etc., and assign to it the three families given by Andres, viz.: the Zoanthidæ, the Bergidæ, and the Sphenopidæ.

#### Genus ZOANTHUS (Cuv.), Erdmann.

Zoanthidæ with fleshy walls, there being no sand or foreign matter imbedded in the mesoglœa; the cœnenchyma is stolon-like, with a slight tendency to form plate-like expansions. The mesenteries are arranged on the microtypus, and the sphincter muscle is imbedded in the mesoglœa and is double.

The synonymy of this genus, as indeed that of all the genera of the Zoanthidæ, is very much confused, and instead of giving it in full, I have thought it better to present in a concise form the limitations of the genus as given by the principal authorities.

I. Actinians united in considerable numbers on a common base — Cuvier ('17), Gosse ('60).

II. Actinians with the individuals united by stolon-like prolongations — Lesueur ('17), Ehrenberg ('34), Dana ('46), Milne-Edwards ('57), Duchassaing and Michelotti ('60), Gray ('67), Verrill ('68), Hertwig ('82).

III. Colonial actinians with fleshy walls — Klunzinger ('77), Andres ('83).

IV. As defined above — Erdmann ('85).

The arrangement of the mesenteries in *Zoanthus* was first accurately made out by R. Hertwig ('83), and his results were later confirmed by G. Müller ('84), Erdmann ('85), and W. Koch ('86). Erdmann, however, first made this arrangement, taken in connection with the nature of the sphincter, of generic importance, separating forms in which, like *Zoanthus*, the second pair of mesenteries in each side, counting from the micro-directives, consists of a macro- and a micro-septum, from those in which the

corresponding pair, as in *Palythoa*, consists of two macrosepta. The former arrangement he terms the microtypus, and the latter the macrotypus.

12. *Zoanthus sociatus* (Ellis), Lesueur. (Pl. II., Fig. 3; Pl. IV., Figs. 15-18.)

*Synon.* — *Actinia sociata* — Ellis, 1767.

*Zoanthus sociatus* — Cuvier, 1817.

*Zoanthus sociata* — Lesueur, 1817.

*Zoanthus socialis* — Blainville, 1830 (teste Andres).

*Zoanthus Ellisii* — Bosc, 1802.

*Zoantha nobilis* — Duchassaing and Michelotti, 1860.

This is one of the earliest non-European Actinians which has been described, Ellis having described it in 1767. His description, however, is principally anatomical, and sufficient is not given to distinguish it from other species of *Zoanthus*. In the edition of Ellis' studies on the Corallines compiled by Solander ('86) it is suggested that this form may be identical with the "Waterbottles" described by Hughes in his Natural History of the Barbadoes, published in 1750. Lesueur ('17) employed Ellis' name for a species which he characterizes with considerable clearness, and there is little doubt but that the form described below is identical with his species. Duchassaing and Michelotti ('60) describe a form, *Z. nobilis*, giving as a synonym for it *Z. sociata* (Les.), and stating that their form differs from Lesueur's in having the tentacles longer and more numerous, and of a blue color, instead of yellow; but it seems probable that the two are identical, the difference in coloration being comparatively unimportant. Bosc's name was applied to the *Actinia sociata* of Ellis.

This species was very common at New Providence, growing in masses as much as 15 cm. in diameter. It seems to be widely distributed throughout the West Indies, since, if the synonymy given above be correct, it has been described from Barbadoes, Dominica, and Guadaloupe. In color (Pl. II., Fig. 3), the stolon and lower part of the column is usually flesh-colored, while the upper part of the column is purplish brown; the tentacles are the same color as the upper part of the column, while the disc is bright green, sometimes varying to peacock-blue or pale bluish green; in many forms there were two tri-



angular brown spots upon the disc, each with its apex at the angle of the mouth, the base resting upon the margin.

The stolons in section (Pl. IV., Fig. 16) are seen to contain a cavity into which numerous small mesenteries project from the wall, being arranged as in the body of the polyp. The stolons are evidently elongations of the column of a polyp; the polyp becomes as it were very much drawn out in its lower portion, which becomes attached to the surface of the rock and gives support to the upper portion, rising up at right angles to it. It is to be noted that the formation of new polyps by budding does not take place from the stolon, but from the base of the polyp proper; *i.e.*, from the region where the polyp joins the stolon.

The polyps measure from 0.9 cm. to 1.25 cm. in height, and at the top about 0.4 cm. in diameter, tapering off somewhat below; in contraction they are club-shaped. The outside of the column is covered by a well-marked cuticle (Pl. IV., Fig. 15, *cu*), to which foreign bodies, such as diatom frustules, etc., are attached. This cuticle is no doubt a secretion of the ectoderm cells (*ec*), which, in the specimens examined, seem to have become fused to form a vacuolated layer, in which are numerous nuclei and strands of granular protoplasm. The mesogloea of the column wall measures 0.06–0.08 mm. in thickness, becoming, however, thicker above, and presents the usual structure described by Hertwig ('83) and Erdmann ('85). The endoderm is thin, measuring only  $8\mu$ – $12\mu$ , and is densely packed with "yellow cells." The general musculature of the column is very weak, the muscle cells forming an almost flat layer. The sphincter is imbedded in the mesogloea and is double, the column wall in contracted individuals being deeply constricted in that region between the two portions, as in the form figured and described by Erdmann. The upper portion is small, and has its muscle fibres running in many cases obliquely, so that a vertical longitudinal section does not show them cut across transversely; the lower portion is long, extending down the column wall for a distance of about 5 mm.

The tentacles are arranged in two cycles, and in the larger polyps number from 44 to 50. Their ectoderm does not possess the cuticle which occurs on the column, but is ciliated. The muscle layer is weak, but still somewhat stronger than that of the column wall. The mesogloea differs from that of column in

not containing any enclosures of ectoderm cells, and the endoderm is much thicker than elsewhere, and is literally loaded with "yellow cells." The disc resembles the tentacles in structure, but the ectoderm cells are less distinct, more nearly resembling those of the column, and the mesogloea contains enclosures of ectoderm cells. The stomodæal ectoderm has no cuticle and is ciliated, and the mesoderm, containing enclosures of ectoderm cells, is thrown into slight longitudinal folds (Pl. IV., Fig. 18).

The mesenteries are arranged on the microtypus (Erdmann), and vary in number according to the size of the polyp, equalling in number the tentacles. The increase in number occurs by the formation of new pairs on either side of the ventral (macro-) directives, as has been described for other *Zoanthidæ* by G. Müller ('84) and Erdmann. The mesogloea is thin, measuring only about  $4\mu$ ; the basal canal is long and not at all wide, producing only a very slight basal thickening of the mesentery (Pl. IV., Fig. 17); and the musculature is weak, forming a single almost smooth layer covering the whole surface of the mesentery, the mesogloea not being raised into folds to support it as in the *Zoanthus* from the Bermudas described by Erdmann. In one mesentery I observed the basal canal communicating with one of the spaces in the mesogloea of the column wall. It seems open to question whether the cells of the larger cavities in the mesogloea are not in reality endodermal in their origin.

In none of the specimens examined were any reproductive organs present.

#### Genus GEMMARIA (Duch. and Mich.).

*Synon.* — *Gemmaria* — Duchassaing and Michelotti, 1860.  
Epizoanthus (in part) — Verrill, 1868.

*Zoanthidæ* with sand or foreign matter imbedded in the mesogloea; the cœnenchyma is absent or lamellar; the mesenteries are arranged on the microtypus, and there is a single sphincter enclosed in the mesogloea.

An arrangement such as is described in the above definition is not included among those given by Erdmann ('85), and I have consequently referred the single form which possesses it to a distinct genus to which I have applied Duchassaing and Miche-

lotti's name *Gemmaria*, since in its general characters the form to be described seems to resemble not a little their *Gemmaria Ruzei*, though differing decidedly from it in coloration. The forms included in the genus as here defined approach *Epizoanthus*, but differ in not incrusting shells, etc., and in having the mesenteries arranged on the microtypus.

13. *Gemmaria isolata*, n. sp. (Pl. II., Fig. 4; Pl. IV., Figs. 19-20.)

I met with this species on a single occasion only, while collecting at the eastern end of Rose Island. The individuals were scattered and buried up to the tentacles in sand. Owing to the depth of the water and the rapid tide I was unable to observe the cœnenchyme, and it is quite possible that the animals may be solitary, though I am inclined to believe that they are connected by a thin continuous lamellar cœnenchyme. A single individual has a bud arising from its base.

The column is cylindrical, broader above than below. In height it measures 2.5 cm., the disc when expanded measuring about 0.8 cm. in diameter. In color the column (Pl. II., Fig. 4) is grayish yellow, owing to the incrusting matter. The disc and tentacles are ochre-yellow, the latter being spotted with white on their inner surfaces. The peristome and mouth are white.

The ectoderm is protected by a not very strong cuticle, and is composed of several rows of cells, presenting an appearance similar to that figured by Erdmann for *Zoanthus*. It measures 0.024-0.04 mm. in thickness. The mesoglœa contains enclosures of foreign bodies—sand, foraminifera and radiolarian shells, and sponge spicules—almost throughout its entire thickness, but towards the upper part these foreign substances are less abundant and are confined to a greater extent to the outer region of the mesoglœa. This layer is about 0.4 mm. in thickness. The sphincter is single and imbedded in the mesoglœa, in its upper part being about half-way between ectoderm and endoderm, but lower down approaching the endoderm so as to be separated from it only by a thin layer. Above it consists of a single row of cavities, few in number, containing muscle cells, arranged in various directions, so that many are cut obliquely; but below (Pl. IV., Fig. 19) it consists of a single row of circu-



lar cavities, apparently without any muscle fibres and with a darkly staining border.

The tentacles are rather short and somewhat acuminate, and are arranged in two cycles, there being from 31 to 34 in each cycle. The disc has its mesoglœa densely loaded with enclosed cavities, containing cells probably ectodermal and muscular in their nature (Pl. IV., Fig. 21). The stomodæum (Pl. IV., Fig. 20) is peculiar in being rounded at its dorsal edge, but abruptly truncated at the ventral or gonidial edge, the directives being attached one to each angle formed by the truncation.

The mesenteries are arranged on the microtypus and are very slender, the musculature being only slightly developed and arranged as in *Zoanthus sociatus*. The basal canal in many cases forms a circular cavity similar to those forming the greater portion of the sphincter, but in the majority of cases is slender and produces only a slight enlargement of the base of the mesentery. None of the specimens examined possessed reproductive organs.

#### Genus CORTICIFERA (Les.), Erdmann.

*Synon.* — *Palythoa auct.*

Zoanthidæ, with sand or foreign matter imbedded in the mesoglœa, and the polyps imbedded throughout their greater extent in cœenchyma; sphincter muscle single enclosed in the mesoglœa; mesenteries arranged on the microtypus.

This term was first proposed by Lesueur ('17) for the reception of the Zoanthidæ, in which the polyps were imbedded nearly to the tentacles in a cœenchyma. Later the term *Palythoa* was limited so as to include forms with this characteristic (Verill '68 and Gray '67), and Lesueur's term passed out of use, but has been revived again by Erdmann ('85).

#### 14. *Corticifera flava*, Les.

*Synon.* — *Corticifera flava* — Lesueur, 1817.

*Palythoa* (*Corticifera*) *flava* — Duchassaing and Michelotti, 1860.

*Palythoa mammosa*, *var. flava* — Duchassaing and Michelotti, 1866.

This form was very abundant at New Providence, forming colonies of from 15–22.5 cm. in length by from 7.5–12.5 cm. in breadth in the shallow water along the shores. I identify it

with Lesueur's *Corticifera flava* ('17) with tolerable certainty. I was inclined for a time to consider it identical also with the form described by Ellis and Solander ('86) under the name *Alcyonium mammillosum*, but there is too much uncertainty regarding this form. Dana ('46) and Milne-Edwards ('57) believe this to be a form in which the polyps project somewhat above the surface of the cœenchyma, a conclusion no doubt derived from the figure given by Solander. I think, however, it would be as well to allow Ellis and Solander's name to lapse altogether, since the description which they give is not sufficient to allow of certainty in the identification of any form with it, and has already given rise to some confusion.

Andres identifies Lesueur's species with Klunzinger's *Palythoa tuberculosa* ('77) from the Red Sea. Müller ('84) has described the arrangement of the mesenteries of this form, and, as will be seen, it differs in some respects from the Bahama form. Erdmann, too ('85), has given a brief description of a form from Simons' Bay, Cape of Good Hope, which Hertwig ('88) identifies with Klunzinger's *Palythoa tuberculosa*, and this also disagrees in some points, both with Müller's description and with the Bahaman species. It seems doubtful accordingly if the identifications of Hertwig and Andres are correct.

In *C. flava* the polyps are deeply imbedded in the cœenchyma and are separated from each other by slight intervals of that tissue, so that their outline is circular and not polygonal from mutual pressure, as in Hertwig's *C. tuberculosa*. In preserved and therefore contracted specimens the height of the individual polyps is about 1.5 cm. and the breadth 0.5 cm., agreeing in this respect with Müller's form, but differing from Hertwig's, the measurements of which are respectively 6-8 mm. and 5 mm. In the expanded condition the disc of *C. flava* measures 0.8 cm. in diameter. The small portion of the polyps which extend above the cœenchyma forms in preserved specimens a ring-like swelling, the surface of which is marked with radiating furrows, which in expanded individuals may be seen to extend to the margin, separating there 16-18 tubercles. This character seems to be possessed also by Klunzinger's and Hertwig's forms, and this appears to have been the principal reason for the fusion by Andres of Lesueur's and Klunzinger's species.

The basal member of the cœenchyma is not particularly

thick, but is of smaller extent than the upper surface of the colony; in consequence of this the polyps towards the periphery of the colony approach more or less a horizontal position.

The ectoderm of the polyps is protected by a cuticle, and consists of several rows of cells as in *Gemmaria isolata* and the *Zoanthus* from the Bermudas described by Erdmann. The mesoderm is thickly studded with imbedded foreign substances, such as grains of sand, foraminiferal and radiolarian shells, and sponge spicules, a thin layer only, adjacent to the endoderm, being free from these bodies. Neither Hertwig nor Erdmann makes any definite statement regarding the arrangement of these imbedded particles in their *C. tuberculosa*, merely stating that in its anatomical characters it agrees with the Bermuda form which Hertwig identifies with Quoy and Gaimard's *P. lutea*. In this the foreign particles are limited to a small region of the mesogloea immediately below the ectoderm and to the coenenchyma between the polyps, being here scattered; elsewhere the mesogloea is soft. I was not able to detect in the Bahama form any of the definitely shaped calcareous bodies with a radiating structure which Müller and Klunzinger describe as occurring in *P. tuberculosa* and which remind one of Alcyonarian spicules. The mesogloea, as in other Zoanthidæ, contains numerous endodermal canals and isolated ectodermal cell-islands as well as the connective tissue cells. The sphincter resembles closely that of *Gemmaria*, differing from it only in that there are a greater number of spaces filled with muscle cells towards its upper end.

The margin of the polyps, as stated above, is tuberculate, the tubercles varying in number from 16-18. The tentacles vary in number, the largest polyps possessing 36-40 arranged in two cycles. The disc is concave, and the peristome elevated and provided with minute white tubercles. The stomodæum resembled that of *Gemmaria* in shape. (See Pl. IV., Fig. 20.)

The mesenteries are arranged on the microtype, and were delicate with weak musculature. Unfortunately, the material I brought back with me was not preserved sufficiently well to allow a study of the histology of the internal parts. I did not observe any reproductive organs in the forms examined. Müller states that in *P. tuberculosa* the mesenteries unite at the



base of the polyp to form a more or less retiform tissue. This does not seem to be the case in the Bahama form. The endoderm of the mesenteries is pigmented.

The entire colony was of a sandy yellow color, the disc being darker, verging towards brown.

### Tribe CERIANTHEÆ.

Actiniaria with numerous unpaired mesenteries and a single ventral gonidial groove; the mesenteries are longest on the ventral side and diminish gradually towards the dorsal aspect; the two mesenteries attached to the bottom of the gonidial groove (the directives) are remarkably small, and are distinguished in this way from the other ventral septa (Hertwig).

I was not successful in obtaining any members of this tribe, but Dr. H. V. Wilson discovered several free-swimming larvæ belonging apparently to a species of *Cereanthus*.

I wish to add a few remarks of a general nature which have been suggested by the studies, the results of which are given in the preceding pages.

I was much struck by the resemblance which the Actinarian fauna of the Bahamas presents to that of the Pacific, and its decided difference from that of the eastern coast of America. It must be granted of course that little is known regarding the Actinology of the Gulf of Mexico and of the Central and South American coasts, but on the other hand the Actinians occurring on the Atlantic coast of the United States as far south as Charleston, S. C., are well known, and the dissimilarity of the Bahama forms to these is very apparent. To make a generalization, we may say that the Actinian fauna of the Pacific differs from that of the Atlantic in the greater number of Stichodactylinæ and Thalassianthinæ which it contains, and the number of forms of the former sub-tribe occurring in the Bahamas is very noticeable. It seems that so far as the Actiniaria are concerned two great areas of distribution can be defined, — the Indo-Pacific, including the Indian and Pacific oceans and the seas connected with them, such as the Red Sea; and the Atlantic, including in this the Mediterranean. The Caribbean region of the Atlantic is, however, to be separated from the Atlantic region and united

with the Indo-Pacific, the relationships of its Actiniaria being very certainly with those of that region. How far this may hold in the case of other animal groups remains to be seen, and to enter into the question fully would be beyond the scope of this paper. It may be noted, however, that von Lendenfeld, in a recent paper<sup>1</sup> states that the Fibrospongiæ of the Atlantic region of North America (from the context I presume he means more especially the West Indian region) and of the East African region are most nearly related to the Australian forms. He also states, however, that there is more similarity between the North American and Australian forms of this group, than between those of the latter region and those of the northeastern portion of the Indian Ocean.

Of the tribe Hexactiniæ the sub-tribe Actininæ has representatives in both regions, and the similarity in genera is quite evident. The Stichodactylinæ are, however, much more abundant in the Indo-Pacific (including in this the Caribbean region) than in the Atlantic. Of the families of this tribe the Corynactidæ occurs in both regions, and the Aurelianidæ in the Atlantic region only, unless the *Actinoporus elegans* of Duchassaing and Michelotti ('60) and the *Actinia osculifera* of Lesueur ('17), which occur in the West Indies, are, as Andres thinks, Aurelians. This seems very doubtful, however. The other families, Discosomidæ, Rhodactidæ, Phymanthidæ, Phyllactidæ, Crambactidæ, and Criptodendridæ, are unrepresented in the Atlantic region (excluding the Caribbean area), and of these all but the last two are represented in the West Indies. The similarity of many of the West Indian genera to those of the Red Sea is especially remarkable. Thus *Discosoma anemone* is most nearly related to *D. giganteum* of Klunzinger. The only two species of *Rhodactis* known, *R. rhodostoma* and *R. Sancti Thomæ*, occur respectively in the Red Sea and in the West Indies; *Heteranthus floridus* is closely related to Klunzinger's *H. verruculatus*; and of the Actininæ, *Condylactis passiflora* is related to Klunzinger's *Paractis erythrosoma*.

The only forms found by me at the Bahamas which are characteristically Atlantic, are the Aiptasias, *Bunodes tæniatus* and *Aulactinia stelloides*.

<sup>1</sup> R. von Lendenfeld. — Der Charakter der australischen Cölenteratenfauna. *Biolog. Centralbl.*, VII., 1887-88.

The occurrence of *Lebrunea neglecta* in shallow water in the West Indies is of considerable interest in view of the fact that the other members of the sub-tribe Dendromelinæ, so far as is known, occur in deep water — 2160 and 1375 fathoms — off the coast of Chili. I think there can be little doubt but that Hertwig's *Ophiodisci* are related to *Lebrunea* in the possession of the peculiar pseudotentacles; and this being the case, we have two related genera, the only ones known of the family, living under conditions apparently totally different. *Ophiodiscus* lives in a region in which prevail absolute darkness, almost total stillness, and a comparatively very low temperature, whereas *Lebrunea* is exposed to the full light of the sun, to water constantly in motion, and to a perennially high temperature. This seems at first sight to be a decided anomaly, but I think an explanation is to be found in a suggestion made by Semper.<sup>1</sup> He has shown that a great number of genera of Holothuridæ, which were generally supposed to be boreal, living at considerable depths in northern seas, occurred in the Philippines, and only at a moderate depth. The conclusion follows that it is not so much the absolute temperature which limits the distribution of animals as the exposure to great or more or less sudden variations. Although the absolute temperatures to which *Lebrunea* and *Ophiodiscus* are exposed differ enormously, yet in both cases it is an equable temperature, an almost constant great degree of cold in the case of the latter, while *Lebrunea* lives in the warm waters of one of the most equable climates known.

To return to the question of distribution, I think that the relationships of the West Indian Actiniaria to those of the Pacific is another piece of evidence in favor of a past communication between the Atlantic and Pacific oceans through the Isthmus of Panama. It is a case in accordance with what is known regarding the similarities in the fishes, mollusca, and Holothurians of the two sides of the Isthmus.

November 21, 1888.

<sup>1</sup> C. Semper, *Reisen im Archipel Philippinen*. Theil II., Bd i. "Holothurien." Wiesbaden, 1868.



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## EXPLANATION OF PLATES.

*D* & *D'* = directive mesenteries.  
*ec* = ectoderm.  
*en* = endoderm.  
*go* = gonidial groove of stomodæum.  
*m* = muscle cells.  
*mec* = modified ectoderm.  
*mel* = elevations of mesogloea.  
*mes* = mesentery.  
*mgl* = mesogloea.  
*mp* = muscle processes of mesogloea.

*n* = nerve layer.  
*pbm* = parieto-basilar muscle.  
*st* = stomodæum.  
*sp* = sphincter muscle.  
*t* = tentacle.  
*ver* = verruca.  
*yc* = yellow cells.  
 I., II., III., IV., V. = the cycles of mesenteries.

## DESCRIPTION OF PLATE I.

(All the figures are natural size.)

- FIG. 1. *Aiptasia annulata* (Les.), And.  
 FIG. 2. *Aiptasia tagetes*, var. *a*, *spongicola*.  
 FIG. 3. *Condylactis passiflora*, Duch. and Mich.  
 FIG. 4. *Bunodes taniatus*, *n. sp.*  
 FIG. 5. *Aulactinia stelloides*, *n. sp.*  
 FIG. 6. Sextant of disc of *Aulactinia stelloides*.  
 FIG. 7. *Lebrunea neglecta*, Duch. and Mich.  
 FIG. 8. *Discosoma anemone* (Ellis), Duch.  
 FIG. 9. *Rhodactis Sancti Thomæ* (Duch. and Mich.).  
 FIG. 10. *Heteranthus floridus* (Duch. and Mich.)















## DESCRIPTION OF PLATE II.

(All the figures are natural size.)

- FIG. 1. *Phymanthus crucifer* (Les.), And.  
FIG. 2. *Oulactis flosculifera* (Les.), Duch. and Mich., partly expanded.  
FIG. 3. *Zoanthus sociatus* (Ellis), Les.  
FIG. 4. *Gemmaria isolata*, n. sp.











## DESCRIPTION OF PLATE III.

FIG. 1. Transverse section of directive mesentery of *Aiptasia annulata*.  $\times 30$ .

FIG. 2. Transverse section of mesentery of I. cycle of *Aiptasia tagetes*.  $\times 44$ .

FIG. 3. Diagrammatic transverse section of column of *Aiptasia tagetes*, showing the arrangement of the mesenteries.

FIG. 4. Longitudinal section of the upper part of the column of *Condylactis passiflora*, showing the absence of a special sphincter.  $\times 50$ .

FIG. 5. Portion of a transverse section of a contracted tentacle of *Condylactis passiflora*.  $\times 185$ .

FIG. 6. Portion of a transverse section of a mesentery of *Condylactis passiflora*, showing the arrangement of the mesogloal muscle processes.  $\times 60$ .

FIG. 7. Transverse section of the sphincter muscle of *Bunodes teniatus*.  $\times 45$ .

FIG. 8. Longitudinal section of column wall of *Aulactinia stelloides*, passing through two verrucal tubercles.  $\times 52$ .

FIG. 9. Transverse section of sphincter muscle of *Aulactinia stelloides*.  $\times 60$ .

FIG. 10. Diagrammatic transverse section of a sextant of the column of *Aulactinia stelloides*, to show the arrangement of the mesenteries.

FIG. 11. Pseudo-tentacle of *Lebrunea neglecta*, expanded. Natural size.

FIG. 12. Transverse section through the basal portion of the pseudo-tentacle of *Lebrunea neglecta*.  $\times 41$ .

FIG. 13. Transverse section through a tentacle, towards its tip, of *Lebrunea neglecta*.  $\times 114$ .

FIG. 14. Transverse section through basal portion of mesentery of *Lebrunea neglecta*.  $\times 72$ .

FIG. 15. Transverse section of sphincter muscle of *Discosoma anemone*.  $\times 65$ .

FIG. 16. Longitudinal section through column wall of *Discosoma anemone*, to show the elevations of the mesogloea.  $\times 83$ .















## DESCRIPTION OF PLATE IV.

FIG. 1. Portion of transverse section through a mesentery of *Discosoma anemone*.  $\times 59$ .

FIG. 2. Portion of tangential section through disc and column of *Rhodactis Sancti Thomæ*, just below the bases of the marginal tentacles. *en*=endoderm of column; *en'*=endoderm of disc; *ec*=ectoderm of disc; *ne*=large nematocyst in endoderm.  $\times 123$ .

FIG. 3. Portion of transverse section through the stomodæum of *Rhodactis Sancti Thomæ*.  $\times 45$ .

FIG. 4. Portion of transverse section through the body wall of *Heteranthus floridus*.  $\times 44$ .

FIG. 5. Longitudinal section through a disc tentacle of *Heteranthus floridus*.  $\times 64$ .

FIG. 6. Transverse section through a verruca of *Phymanthus crucifer*. *py*=pyriform cells (nerve cells?).  $\times 50$ .

FIG. 7. Longitudinal section through the upper portion of the column wall of *Phymanthus crucifer*.  $\times 50$ .

FIG. 8. Transverse section through a tentacle of *Phymanthus crucifer*. *mgl*=thickened mesogloea.  $\times 16$ .

FIG. 9. Portions of transverse section through a mesentery of *Phymanthus crucifer*: *a*, near its base; *b*, near its middle.  $\times 35$ .

FIG. 10. Transverse section through gonophoric region of a mesentery of *Phymanthus crucifer*. *te*=testis; *fi*=filamental apparatus.  $\times 250$ .

FIG. 11. Longitudinal section through a disc tentacle of *Phymanthus crucifer*.  $\times 100$ .

FIG. 12. Portion of longitudinal section of column wall of *Oulactis flosculifera*, to show elevation of the mesogloea.  $\times 56$ .

FIG. 13. Portion of transverse section of a tentacle of *Oulactis flosculifera*.  $\times 72$ .

FIG. 14. Transverse section through the gonidial groove of the stomodæum of *Oulactis flosculifera*.  $\times 25$ .

FIG. 15. Portion of transverse section through the column wall of *Zoanthus sociatus*. *cu*=cuticle; *enc*=endodermal canal in mesogloea.  $\times 265$ .

FIG. 16. Transverse section of stolon of *Zoanthus sociatus*.  $\times 30$ .

FIG. 17. Transverse section of basal portion of macroseptum of *Zoanthus sociatus*. *bc*=basal canal.

FIG. 18. Transverse section of stomodæum of *Zoanthus sociatus*.  $\times 33$ .

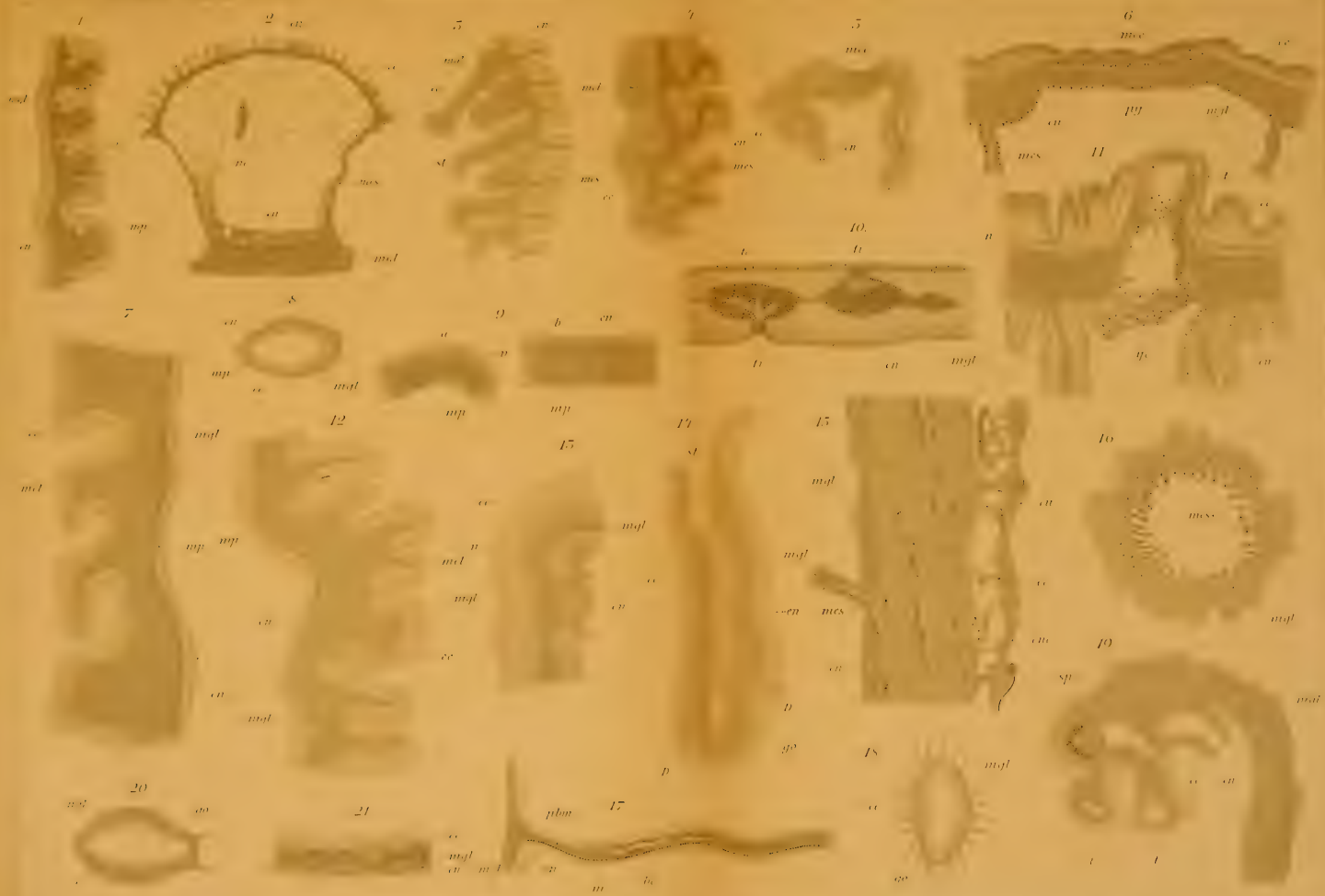
FIG. 19. Longitudinal section through margin and upper part of column wall of *Gemmaria isolata*, showing the sphincter muscle.  $\times 25$ .

FIG. 20. Transverse section of the stomodæum of *Gemmaria isolata*.  $\times 27$ .

FIG. 21. Radial section of disc of *Gemmaria isolata*.











# CONTRIBUTIONS TO THE COMPARATIVE OSTEOLOGY OF THE FAMILIES OF NORTH AMERICAN PASSERES.

R. W. SHUFELDT, M.D., C.M.Z.S.

Two years ago, when our Ornithologists' Union published its official avifaunal List of American Birds, the Order PASSERES was made to contain four hundred and thirty-two (432) species and sub-species,<sup>1</sup> which formidable array is therein duly divided and subdivided into its sub-orders, families, sub-families, genera, and so on. It would be far exceeding the scope of the present memoir to present a detailed scheme of the classification adopted by the Union for this extensive group of birds; much less would it be appropriate for the writer to undertake to offer here a complete list of these forms, giving the name of each species, as the reader can, by a brief perusal of the work referred to, soon obtain a comprehensive idea of such matters. As we propose to deal here with the osteology of the FAMILIES only, I present, as a mere matter of convenience, the ORDER below, with its divisions through those groups; and a glance at this scheme of the Order, as given, shows us that we have twenty (20) Families of these North American Passeres to be taken into consideration, and it may be as well to add here that the number of species, however, contained in any single family or group varies considerably; and we see, for example, such a family as the *Cinclidæ* represented by but a single species, while, on the other hand, such a family as the *Fringillidæ* contains upward of a hundred and forty species or more.

<sup>1</sup>The Code of Nomenclature and Check-List of North American Birds adopted by the American Ornithologists' Union. New York, 1886. In this work the term "North American," as applied to its List of Birds, is held to include the continent of North America north of the present United States and Mexican boundary, as well as Greenland, and the peninsula of Lower California, with the islands naturally belonging thereto.

ORDER.	SUB-ORDERS.	FAMILIES.	Includes
Passeres.	Clamatores.	1. Tyrannidæ.	Tyrant Flycatchers.
		2. Alaudidæ.	Larks.
		3. Corvidæ.	Crows, Jays, and Magpies.
		4. Sturnidæ.	Starlings.
		5. Icteridæ.	Blackbirds, Orioles, etc.
		6. Fringillidæ.	Finches, Sparrows, etc.
		7. Tanagridæ.	Tanagers.
		8. Hirundinidæ.	Swallows.
		9. Ampelidæ.	Waxwings, etc.
		10. Laniidæ.	Shrikes,
	Oscines.	11. Vireonidæ.	Vireos.
		12. Cœrebidæ.	Honey Creepers.
		13. Mniotiltidæ.	Wood Warblers.
		14. Motacillidæ.	Wagtails.
		15. Cinclidæ.	Dippers.
		16. Troglodytidæ.	Wrens, Thrashers, etc.
		17. Certhiidæ.	Creepers.
		18. Paridæ.	Nuthatches and Tits.
		19. Sylviidæ.	Warblers, Kinglets, Gnatcatchers.
		20. Turdidæ.	Thrushes, Solitaires, Stonechats, Bluebirds, etc.

These Families, then, are presented in the order in which they appear in the A. O. U. Check-List, and as the systematists who compiled that work declare that "the List [is] to begin with the lowest or most generalized type, and end with the highest or most specialized" (p. 15), it is but fair to presume that as the families begin with the *Tyrannidæ* and conclude with the *Turdidæ*, the former were considered to be the "most generalized types," the latter the "most specialized," while the eighteen families, serially arranged between these extremes, hold their several positions in recognition of this plan.

For the past ten years the present writer has been gradually collecting together, in various parts of the United States and from various sources, osteological material illustrative of the group of passerine birds; so that at this writing we have before us a very fair representative line of such skeletons. And with but few exceptions, every family in the above list is in this way at our hand, and the missing forms are from groups, the species of which come to us usually only as stragglers, or casuals, as *Sturnus vulgaris* and the Bahama Honey Creeper (*C. bahamensis*), but no others.

It is our aim in the present connection to place before the reader a brief, concise sketch of the osteology of one or more species of as many of these passerine families as possible, and as such work proceeds, compare the salient features of the skeleton of any family with the corresponding ones as found in species of another or other family or families supposed to be more or less nearly affined. Possibly by such means we may be enabled to point out, so far as skeletal characters are concerned, the relations that some of the groups of this always puzzling order to the taxonomist apparently bear to each other, though no one is better aware than the writer that such complex questions can never be fully determined until the morphology of each and *all* the species of the *Passeres* is worked carefully out in its minutest details, and this we have spoken of again and again in our published memoirs. It is earnestly hoped that the work here undertaken may assist matters to that end, and will to some degree supplement the able endeavors of former authors in the same field.<sup>1</sup>

Few ornithologists better appreciate the difficulties which still stand in the way of a correct classification of the order *Passeres* than my friend Professor Newton, and this distinguished authority has said that, in referring to this group, "Some two or three natural, because well-differentiated, families are to be found in it, — such, for instance, as the *Hirundinidæ*, or Swallows, which have no near relations; the *Alandidæ*, or Larks, that can be unfailingly distinguished at a glance by their scutellated *planta*, as has been before mentioned; or the *Meliphagidæ*, with their curiously constructed tongue. But the great mass, comprehending incomparably the greatest number of genera and species of birds, defies any surer means of separation. Here and there, of course, a good many individual genera may be picked out capable of most accurate definition; but genera like these are in the minority, and most of the remainder present several apparent alliances, from which we are at a loss to choose that which is nearest. Four of the six groups of Mr. Sclater's 'Laminiplanter' *Oscines* seem to pass almost imperceptibly into one another. We may take examples in which what we may call the Thrush form, the Tree-creeper

<sup>1</sup> MCGILLIVRAY, W., *British Birds*, I., pp. 485, 486; and PARKER, W. K., *Trans. Zööl. Soc.*, V., p. 150.



form, the Finch form, or the Crow form, is pushed to the most extreme point of differentiation; here we shall find that between the two outposts thus established there exists a regular chain of intermediate stations, so intimately connected that no precise lines of demarcation can be drawn cutting off one from the other."<sup>1</sup>

Now these observations apply nowhere more cogently than they do in the study of the osteology of the *Passeres*, and it is positively almost beyond the range of possibilities, sometimes, to distinguish between the skeletons of certain closely related species, while in other instances very excellent differentiating characters may be found; and these latter will be brought conspicuously into the foreground and made the most of, when met with. It matters but little which family we select to commence this series of osteological comparisons of this order of birds, though for convenience' sake, solely, the writer proposes to take the genus *Sialia* of the family *Turdidæ* first in order, because on this occasion it is desirable to follow the sequence adopted by the A. O. U. Check-List. Not that we are at all convinced that the *Turdidæ* constitute the most highly specialized group of birds in our avifauna, for we have decided opinions and leanings quite the converse to any such an hypothesis; but more for the reason that we find in such a skeleton as is furnished us by *Sialia* a type, as it were, of what we have been given to understand the passerine skeleton, through the numerous descriptions of a host of former anatomists, purports to be.

We have divided our *Turdidæ* into two sub-families—the *Myadestinæ* and the *Turdinæ*; the first containing the genus *Myadestes*, and represented by the sole species *M. townsendii*, and the second the genera *Turdus*, *Merula*, *Hesperocichla*, *Cyanocula*, *Saxicola*, and *Sialia*,—each containing one or more well-known species of Thrushes or Thrush-like birds.

There are four species of Bluebirds in the genus *Sialia*, and I have compared the skeletons of all. It is hardly necessary to say that in these several species the skeleton is essentially the same, although one might, after long and careful study and comparison, be enabled to pick out those belonging to the different varieties. In the most typical species, each seems to possess

<sup>1</sup> NEWTON, ALFRED, F.R.S., etc., etc., Article "Ornithology," *Brit. Encycl.*, 9th ed., Vol. XVIII., p. 47. 1885.

in its skeleton a *facies* peculiar to itself, but often difficult to satisfactorily describe.

In another connection the writer has already presented a view of the *superior aspect of the skull* in *Sialia mexicana*, so it will not be necessary to re-describe it here.<sup>1</sup> Upon the lateral aspect of this part of the skeleton in the Bluebirds, we are to note the large subelliptical aperture of the external nares, and the complete absence of any osseous septum between it and the corresponding opening on the opposite side. The superior osseous mandible is somewhat curved, tapers smartly to its apex, and is possessed of cultrate tomia. Standing as a good-sized bony partition, we have a quadrilateral *os plana* or *pars plana* dividing, as usual, the rhinal chamber from the orbit, while in nestling specimens of any of the *Sialia*, we find in front of this a large and free lacrymal bone, much as it occurs in the *Corvidæ*; here, however, this ossicle completely fuses with the *pars plana* by the time the bird has fully matured, which is not the case among the Crows.<sup>2</sup>

Bluebirds, as is the rule among most, if not all, true *Turdidæ*, have capacious orbital cavities, with a very deficient bony septum dividing them. This deficiency is due to a sizable vacuity which occupies its central part, while the opening for the first pair of nerves is unduly large, and encroaches to no small degree upon the upper part of the interorbital septum. Notwithstanding these facts, in most specimens the foramina rotunda remain both distinct and entire. Passing to the posterior lower marginal boundary of an orbit, it is seen that neither the sphenotic nor the squamosal process in *Sialia* is very well developed; the latter being rather the better of the two, projecting out as it does over the mastoidal head of the quadrate on either side.

<sup>1</sup> SHUFELDT, R. W., "Notes upon the Osteology of *Cinclus mexicanus*" *Bull. Nutt. Ornith. Club*, Cambridge, Mass. Vol. VII., No. 4, Oct., 1882, pp. 213-221, Fig. B. The same figure is also given in Coues' *Key to North American Birds*, 2d ed., p. 241.

<sup>2</sup> SHUFELDT, R. W., "On a Collection of birds' sterna and skulls, collected by Dr. Thomas H. Streets, U. S. Navy." *Proc. U. S. Nat. Mus.*, 1887, pp. 376-387. The lacrymal bone in the Raven *C. corax sinuatus* is alluded to here, but is more fully described in a paper by the writer, which we will have occasion to quote further on. The morphology of the lacrymal bones stands in some need of more careful research among the *Passeres*; and for the class at large it is subject to a wonderful series of variations. To instance this, we have but to compare the lacrymal in such forms as *Ortyx*, *Anas*, and *Sturnella*.

Huxley long ago drew up for us in the most lucid terms his excellent description of the salient characters to be found upon the basal aspect of the skull of an average passerine bird, leaving but little to be done here beyond instituting certain minor comparisons, and further on, pointing out exceptions to his general rule, which more recent investigations have brought to light.<sup>1</sup> *Sialia* is strictly passerine in the structure of these parts, especially in the form of the *vomer*, as Professor Huxley describes that bone in the work just quoted. In a specimen of *Sialia mexicana*, however, the *maxillo-palatines* are peculiar; their stems being markedly slender, while their mesial free ends are bulbous and hollow, with a full opening, in either one, to the outer side.

In a specimen of *Sialia arctica*, a nestling, these bones have much the same form, though the free ends are not as bulbous at this age, and they come in contact, on either side, with the pointed free anterior end of the inner lamina of a palatine. As the form of the skull changes, due to advancing age, these elements recede from each other, so that in adult specimens no such relation is ever discernible. A *palatine* is characterized in having its lamina very short in the antero-posterior direction; the postero-external angles rounded; and the premaxillary process long and slender, being widely separated from the fellow of the opposite side. The rostrum of the sphenoid is rounded, thick, and stout; while each *pterygoid* is comparatively long and slender; and a *quadrate* wide in its transverse direction. Nothing need be said as to the manner of articulation among the bones I have mentioned, as in each case it is strictly passerine in *Sialia*, and we have been long fully informed upon such matters.

We find nothing beyond what is already known to us in the internal aspect of the cranial casket of a Bluebird, nor in the sclerotals of its eyeballs, its ossicula auditus, the sesamoids posterior to the mandibular articulations, nor in its hyoidean apparatus.

<sup>1</sup> HUXLEY, THOS. H., F.R.S., etc., "On the Classification of Birds; and on the Taxonomic Value of the modifications of certain of the Cranial Bones observable in that class." *P. Z. S.*, 1867, pp. 450, 451. And to enlist a foot-note of Prof. Huxley's, as the works are not at my hand, the reader is also invited to refer to Nitzsch, "Ueber die Familie der Passerinen," in the *Zeitschrift für die gesammten Naturwissenschaften*, 1862, and the article "Passerine" in Ersch and Gruber's *Encyclopædie*, 1840.



Feebleness of structure seems to characterize its *mandible*, or rather that bone throughout the genus; it being of the typical V-shape pattern, with shallow ramal sides, having rounded upper and lower margins; a conspicuous, sub-elliptical ramal vacuity on either side; while the bone as a whole shows a slight though abrupt flexure downwards just beyond its middle. As for the symphysis, it is short, convexed below, concaved above; and at each hinder extremity the articular cup develops a posterior-projecting process, which is directed slightly upwards.<sup>1</sup>

Taking a specimen of *Sialia arctica* as an example, we find that in its *vertebral column* there are 19 vertebræ included between the skull and the pelvis; of these, the first twelve are without free ribs, — the leading minute pair of riblets occurring on the thirteenth vertebra. On the fourteenth vertebra, the pair of ribs, although not connecting with the sternum, are much better developed, and may possess uncinatè processes. The last five free vertebræ of the spinal column are true "dorsals," if we may so nominate vertebræ which support vertebral ribs, that not only have uncinatè processes, but connect through hæmapophyses with the sternum, as these all do. There is also a delicate pair of sacral ribs, which usually are devoid of processes, and whose hæmapophyses fail to reach the costal borders of the sternum. Upon examining specimens of *Merula*, *Turdus*, and *Myadestes*, as well as the Varied Robin (*H. nævia*), I find that they all correspond in this particular with *Sialia*, both as to number of vertebræ, the ribs, and their epipleural appendages. Doubtless it is the formula for all true *Turdidæ*.

Bluebirds have rather a shallow *pelvis*, short in the antero-posterior direction, and with the hind ends of the post-pubis and ischium, on either side, inclined to flare outwards. The ilia are never in contact with each other; quite the reverse, for the groove upon each side of the sacral crista in front is wide, causing the total interval in this region to be quite considerable. In mid-postacetabular space we always find the double row of parial

<sup>1</sup> Since the above was written, an excellent paper has appeared from the pen of Mr. F. A. Lucas, entitled "Notes on the Osteology of the Thrushes, Miminæ, and Wrens" (*Proc. U. S. Nat. Mus.*, 1888, pp. 173-180). It not only contains much osteological information on the groups treated, but is illustrated by a number of useful outline figures, that may well be compared with what we have to say further along.



foramina — the interdiapophysial vacuities among the uro-sacral vertebræ. Viewed laterally, we observe that the obturator foramen and the circular acetabulum are of nearly the same size, while the sub-elliptical ischiadic foramen is about five times as big as the last-mentioned aperture. The obturator space is closed in front, but open behind where the ischium is simply tangent to the slender end of the post-pubis. As near as I can tell from the pelvis of an adult *Sialia*, there appear to be *eleven* vertebræ fused together to form the pelvic sacrum, and they are peculiar in having their common centra flattened upon the ventral aspect, and marked by a double longitudinal row of little squarish pits, from the first to the seventh inclusive.

The first three sacral vertebræ (dorso-sacral) throw out on either side strong diapophysial braces which abut against the ilia; the two succeeding vertebræ lack these, they are aborted; in the sixth and seventh they are long and slender, and again reach out to the ilia as supports opposite the acetabulæ. Thus we see that these birds possess a good average passerine pelvis, and as we proceed occasion will be taken to point out the differences existing in other types and species.

*Six* free vertebræ and the terminal *pygostyle* constitutes the skeleton of the tail in *Sialia*, in all of the specimens I have thus far examined.

Members of this genus possess a *sternum* of a typical passerine pattern, and so well-known is this that it requires no special description from me here. This pattern, I would incidentally remark, — for we will be obliged to return to this subject again in the present memoir, — varies but slightly throughout the entire order of passerine birds, and is markedly uniform in its shape, so that a true species of this enormous group can be diagnosed almost in an instant, and to a certainty by a glance at its sternum. Sir Richard Owen called it the “cantorial sternum,”<sup>1</sup> but this is hardly the proper appellation to apply to it, because the pattern is almost identically the same in the clamatorial birds, and *they* do not sing. (See Fig. 20 of the second Plate to the present paper.)

In *Merula*, the form of the sternum departs but little from the bone in *Sialia*; the “body” perhaps being a little narrower,

<sup>1</sup> OWEN, R., *Comp. Anat. and Phys. of Verts.*, Vol. II., p. 20, Fig. 15.

and the carina a little deeper in proportion.<sup>1</sup> So, too, for all the Sparrows and Finches, the fundamental form is the same throughout,<sup>2</sup> and it is familiar to every tyro in zoölogy.

These Blue Thrushes (*e.g.* in *S. sialia*) possess a *scapula* in their *shoulder girdles* of a very distinctive form, common to them and most true *Turdidæ*. The bone is of the usual passerine pattern, with its posterior fourth somewhat expanded, while the extremity is obliquely truncated from within, outwards, and the terminal apex, drawn out with a little point, is turned somewhat inwards towards the mesial plane.

The *coracoid* is comparatively a long bone with slender shaft, the sternal moiety of which latter always develops an osseous, wing-like expansion, that gradually increases in width from its commencement above, downwards. The head of the coracoid is crooked over toward the mesial plane, and is of tuberos proportions as in most all Thrushes.

The *os furcula* is invariably of the U-shaped form, with its lower half gracefully and gradually curved towards the keel of the sternum; the lower midpoint supporting a conspicuous hypocleidium. The free ends of the limbs of the *os furcula* in *Sialia* are always enlarged, being laterally compressed, and when the bone is articulated *in situ*, they, on either side, are in contact with the head of the corresponding scapula.

Being well known in so far as its skeletal features are concerned, it only becomes necessary to bear in mind the principal points in the osteology of the *pectoral limb* of *Sialia*.

We are to observe the presence of the *os humero-scapulare*, and of the small sesamoid at the elbow-joint, common to most, if not all *Passeres*.

Further, it is to be noted that the bones of this limb, as well as those of the pelvic extremity, are always non-pneumatic, though the pneumatic fossa of the humerus is invariably capacious, and to make it appear more so, the head of the bone curls over an adjacent concavity, juxtaposed to the first-mentioned one. At the lower or distal end of the humerus, an "epicondylloid process" is ever present, while the shaft of the bone is not

<sup>1</sup> See my figure of the sternum of *Merula migratoria* in the second edition of Coues' *Key to North American Birds*, p. 145, Fig. 58.

<sup>2</sup> For a Sparrow, see the figure of the sternum of one of these birds in Prof. M. Harbison's *Elements of Zoölogy*, p. 34, Fig. 9.

as long comparatively as it is known to be in other passerine birds, and in this particular it curiously approaches the Swallows.

Neither *ulna* nor *radius*, nor the ossicles of the carpal joint, present anything worthy of special note. The *carpo-metacarpus* is characterized by a rounded laminar process projecting from the edge of its main shaft upon the palmar aspect, at the proximal third, which slightly overlaps the auxiliary shaft of the bone, or the shaft of the middle metacarpal, which, as we know, fuses with the carpo-metacarpus. Such a process is also present in certain *Gallinæ*, where the writer has figured it.<sup>1</sup>

Two points more: the form of the proximal phalanx of the index digit is to be noted, it being flat upon its palmar, and profoundly excavated upon its anconal aspect; the remaining is, the terminal phalanges of the digits in the *Passeres* do not, so far as I am aware, ever support claws, and to this rule *Sialia* forms no exception.

With respect to the skeleton of the *pelvic limb*, its salient characters are thoroughly known to the morphologist, and we wish here to note simply the fact that in *Sialia*, as in other passerine birds, the *patella* is always present, and the *fibula* always a comparatively short and filliform bone which never fuses with the tibio-tarsus. My memoir on the osteology of *Lanius* gives figures and the usual forms assumed by all these bones of the extremities, and they vary but very little throughout the group.

Figures 3 and 26 of the Plates give views of the *skull* of *Hesperocichla nœvia*, and when we come to compare that part of the skeleton with our skull of *Sialia*, we are surprised to see how much they really are alike; indeed, the skull of the Bluebird would nearly answer for a miniature of the skull of the Varied Robin. It would be sinking quite to trivial details to attempt to enumerate the insignificant departures in one from the other. The superior osseous mandible in *Hesperocichla* is straighter than it is in *Sialia*, and a swell occurs in its tomia beneath the narial apertures (Fig. 26), and were a series of this skull reduced to the size of an equal series of skulls of *Sialia*, this character might be, if constant, sufficiently evident to enable us to make

<sup>1</sup> SHUFELDT, R. W., *Osteology of the North American Tetraonida*, Plate VII., Fig. 58.



a correct diagnosis in differentiating the two series were they mixed up together. Perhaps, too, comparatively speaking, the cranial capacity in such a species as *Sialia mexicana* is greater than it is in *Hesperocichla*, and the day is not far distant when relative size of brain is to be given its weight in determining the position of a bird in the system. Passing to the remainder of the *axial skeleton* in *Hesperocichla*, we find that although it is essentially and fundamentally the same as it is in a Bluebird, yet in its *general facies* it more nearly approaches the corresponding parts of the skeleton in *Merula*. This is quite true of the pelvis and sternum; but at the best the differences among all three are but very slight, and a pelvis of a specimen of *Sialia arctica* in my hand is practically but the pelvis of *Merula m. propinqua* reduced, which I hold in the other, — character for character, — though I believe it is possible there may be one less vertebra in the pelvic sacrum in the *Sialia* than there is in the Robin; but I will not positively vouch for this until I have had the opportunity of counting them in a number of the *nestlings* of the two species.

To all intents and purposes, *Merula migratoria* has a skull and associate structures like those parts in a great overgrown Bluebird, so much are they alike. A good distinguishing feature here, however, are the osseous tympanic bullæ in the Robin, a species wherein they are strikingly conspicuous and large. The truth of this may best be demonstrated by taking an anterior view of the skull of *Merula*, where these bony, flaring ear-couches strike our eye at once, while in *Hesperocichla* and *Sialia* they would hardly attract any special notice. There would be no difficulty in deciding between the skeletons of *Merula* and *Hesperocichla* as to the species they belonged to, — a glance at figures 2 and 3 will satisfy us as to the truth of this, where I have drawn the superior aspects of the skulls of the representatives of these two genera, and similar differences may be detected in the remainder of their skeletons.

*Turdus a. pallasii* as representing its genus has a skeleton the very counterpart of the skeleton in *Hesperocichla*, being in size about one-third less.

Thus it will be seen how, osteologically, our American *Turdinæ* are closely linked together, and they naturally form a very well-defined sub-family of Birds, but I fail to discover anything



in the skeleton of any of them, so far as that part of their anatomy goes, which entitles them to be ranked as the highest forms of the class.

*Myadestes townsendii*, of the remaining sub-family of the *Turdidæ*, is a species that has been made to occupy a number of different positions in the system by various taxonomists; but so far as its skeleton indicates, there can be no doubt but that it is now classified correctly by us. By a glance at figures 1 and 24 of the Plates, one can be at once satisfied that the cranial characters of this bird show it to be nothing more nor less than a true Thrush, though the fore-part of the skull is notably wider than the skulls of the *Turdinæ*; but I would add that the skull of an adult *Myadestes* bears a curious resemblance to the skull of a young *Sialia*, taken at a time when the bird is about ready to quit the nest. For the rest, the skeleton of this Solitaire is pre-eminently turdine, with a few peculiarities which it may claim as its own. The keel of the *sternum* is comparatively shallow, pointing to the fact that *Myadestes* is not a bird of strong flight, which in reality we know to be the case. Already I have shown that in its vertebral column and ribs it agrees with the *Turdinæ*; we may add that it has also *six* free caudal vertebræ and the pygostyle in the skeleton of its tail, and this latter piece is large, and with broad posterior face.

The *pelvis* is peculiar, or at least departs from the more typical thrushlike pattern, in that it has its obturator space and foramen, on either side, not usually separated from each other by an osseous division, and the hinder ends of the post-pubis and ischium fuse with each other. In *Merula* it must be remembered that in its pelvis the ischium always develops a considerable bony span that completely shuts off the obturator space from the adjacent foramen of the same name, and the foot-like posterior end of an ischium never fuses with the post-pubis, though they are closely fitted upon each other. The sixth, seventh, and eighth vertebræ of the cervical division of the spinal column in *Myadestes* are distinguished for the unusual length which their pre- and post-zygapophyses attain, more especially the latter, a fact we cannot fail but notice upon the most casual inspection of this part of the skeleton in the Solitaire.

In a recent report of mine to the American Ornithologists' Union, entitled "On the Position of *Chamæa* in the System,"

and which will appear elsewhere, I have gone over and quite thoroughly presented accounts of the skeleton in the Families *Sylviidæ*, *Paridæ*, *Certhiidæ* and *Troglodytidæ*, so it will not be necessary to reproduce this work in the present connection; suffice it to say that in so far as the first of these families are concerned, the writer has not as yet had the opportunity of investigating the osteology of *Phyllopseustes borealis*, but with respect to the remaining two sub-families of this group, the *Regulinæ* and the *Polioptilinæ*, they seem at present to be classified in accordance with a natural system, and have been assigned places in keeping with their structural characters as we now understand them. In figures 5 and 6 of the Plates, I have drawn superior views of the skulls of a *Regulus* and a *Polioptila*; and although these birds possess a skeleton in each case essentially passerine, it in no way shows any especial affinity with the *Turdidæ*, at least any more than do the skeletons of a number of other representatives of this Order.

*Auriparus flaviceps* of the next following Family, the *Paridæ*, I have never yet had the opportunity to examine,<sup>1</sup> but am fully satisfied that *Chamæa fasciata* is a Tit, that has its nearest affinity in the representatives of the genus *Psaltriparus*,—that is, in so far as I have examined it, and its North American congeners are concerned,—and has, moreover, I think, certain troglodytidine characters still clinging to its organization, which perchance may have been derived from the stock from which *Galeoscoptes carolinensis* sprang, in common with Wrens, Thrashers, and Nuthatches, etc. This may possibly account for *Chamæa* and *Galeoscoptes* being alike in some particulars, as the uniformity of color of their plumage, its laxness, the scutellation of the tarsi being nearly obsolete in each species; somewhat similar habits, and finally both laying *unspotted blue* eggs. Of course should such an affinity exist, it can be but very remote. The

<sup>1</sup> At this point I desire to say that since the above was written I have received a beautiful series of specimens of *Auriparus* from my friend, Mr. Herbert Brown of Tucson, Arizona, who has likewise, with very great generosity, sent me much other material from his region, illustrative of the group of birds we now have under consideration. This and much more will now have to be incorporated in my paper upon *Chamæa*, and a supplementary paper or two which I hope to bring out upon the morphology of the North American Passeres, some time in the future, wherein I intend to compare more thoroughly my work with the published labors of W. K. Parker and others in the same fields.

Chickadees are true Titmice, and in my opinion more highly organized birds than the *Turdidæ*, as they have proportionately larger brains, and in many cases build nests of a high order of architectural design; and, according to Coues, "the young closely resemble the parents, and there are no obvious seasonal changes of plumage."<sup>1</sup> Sub-genus *Lophophanes*, including the Crested Titmice, should be made to constitute the genus *Lophophanes*, as these birds show a very distinct structure from the Chickadees, entitling them fully to generic rank. Indeed, in such a species as the Gray Titmouse (*P. inornatus griseus*), I found, among other distinctive characters, that it had a *vomer* of an oblongate form, being *pointed* in front. This extraordinary fact even constitutes a marked departure from the type that bone assumes among the *Passeres* generally. Huxley laid it down as a law that in the *Ægithognathous* birds "the vomer is a broad bone, abruptly truncated in front, and deeply cleft behind, embracing the rostrum of the sphenoid between its forks."<sup>2</sup> Figures 7, 8, 9, and 10 of the Plates to the present memoir, give superior views of the skulls in Crested Tits, Tits, *Chamæa*, and the Bush Titmice.

Nuthatches (see Fig. 11), as the remaining Family of the *Paridæ*, are possessed of a passerine type of skeleton characterized by a number of features peculiarly its own. *Sitta c. aculeata*, for instance, has the *vomer* very small, though of the usual passerine form; its *lacrymal bones* remain free throughout life, occupying, on either side, a position in front of the *pars plana*, as in certain *Corvidæ*; the interorbital septum is commonly entire, and rather dense; specimens may be met with (I have one before me) wherein the ilia meet at a point over the sacral crista, as in *Chamæa*, and the hinder ends of the ischia are drawn out into unusually slender processes; finally, specimens of this Nuthatch occur in which the "notches" of the sternum are strikingly small. Osteologically, I should say that such a sittatine form as we have here, is not very closely affined to the genus *Lophophanes*, and we may be assured that *good, strong sub-family lines* define their kinship.

Passing to the next family, the *Certhiidæ*, I find I have said in my *Chamæa* essay all that I have to in reference to these

<sup>1</sup> COUES, E., *Key to North American Birds*, 2d ed., p. 263.

<sup>2</sup> *Ibid.*, p. 450.



Creepers; they undoubtedly are entitled to family rank, but I would prefer to devote further research to more extensive material before advancing final opinions upon their definite affinities. In my *Chamæa* paper I give a lateral view of the skull of *C. f. americana*, a species which perhaps has a trace of the Wren in it.

In the same paper I presented the skeletal characters of a number of Wrens and their allies (Family *Troglodytidae*, see Fig. 12), and so will have little or nothing to add about them here. I have examined and carefully compared skeletons of *Mimus*, *Oroscoptes*, *Harporhynchus*, and a number of the true *Troglodytinæ*, and am satisfied that the *Miminæ* are aberrant thrushes, linked with the true *Turdidae* and the Wrens, through such a genus perhaps as *Campylorhynchus*, though *Oroscoptes* has a skeleton that would pass without any difficulty whatever for that of a true turdine type. In my paper on *Cinclus* in the *Nuttall Bulletin*, quoted above, I gave an upper view of the skull of this bird, and one may easily see that I am justified in making this remark. *Mimus* has a skeleton quite like *Oroscoptes*, and fully as Thrush-like. In *Harporhynchus* a decided departure is met with, and the skeletons in some of those species are like skeletons of great overgrown Wrens. They have a peculiar pattern of pelvis, however, essentially their own, which is due to a sharpness of its principal borders and angles, and a certain amount of prominence to its most salient processes.

Still adhering to the plan adopted in the A. O. U. Check-List, the next family we come to is the *Cinclidae*, containing the single species *Cinclus mexicanus*, our American Dipper, and of it I said in my paper on its osteology (*Bull. Nutt. Ornith. Club*, 1882), that it is quite closely related to the genus *Sciurus*, and not far removed from some of the Wrens; while Coues has remarked that this is a "small but remarkable group, in which the characters shared by the *Turdinæ*, *Saxicolinæ*, and *Sylviniæ*, are modified in adaptation to the singular aquatic life the species lead." (*Key*, 2d ed., p. 255.) Now, I have all my old material before me upon which my conclusions were based as given above, and a great deal more besides. I can see in *Cinclus* where I saw the Wren in its skeleton, for in its skull there is that evident resemblance to the turdo-troglodytine stock, while other points clearly show its affinity with the Water Thrushes



(*Sciurus*); and yet, while there is much to base such an opinion upon, the fact still remains that the typical passerine skeleton of *Cinclus mexicanus* is powerfully impressed with strong turdine characters.

My knowledge of the osteology of our American Family *Motacillidæ* rests upon my having carefully studied the skeletons of a number of species of the genus *Anthus*, and such material is before me at the present writing.

The skull in such a form as *Anthus pensilvanicus* is an exceedingly delicate structure in all its parts (Fig. 13), the interorbital septum being markedly deficient in bone; the pterygoids and the zygomæ wonderfully slender rods; while the palatines and premaxillary are about as frail as we ever see them in the Class. Taken as a whole, the skull of this Pipit is almost identically like the skull of *Sciurus motacilla*, while in the rest of its skeleton, more particularly in the sternum and pelvis, we see some rather strong traces of the Thrush: especially is this true of the last-named bone; not in any ways enough, however, to detract from the fact that the *Motacillidæ* see their nearest affinity in the genus *Sciurus* of the *Minotiltidæ*, and the relationship here is very close.

This last-mentioned family is the next one we have in order to consider, and in our American avifauna it is made to contain the Wood-Warblers, a lovely group of birds, that in their structure seem to have a tincture of every morphological variation to be found in the entire passerine order. On p. 287 of the second edition of his *Key*, Coues says of them that "the warblers grade so perfectly towards the tanagers that they have all been made a sub-family *Tanagridæ* (where possibly they belong). The affinity of some of them with *Cærebidæ*, or honey creepers of the tropics, is so close that the dividing line has not been drawn." We well know how *Icteria* branches off in another direction, while the Redstarts are strongly inclined towards the *Tyrannidæ*. True as all this undoubtedly is, we can nevertheless, through a critical examination of a series of skeletons of the genera making up the Family in this country, throw a little light into so closely affined a group, and perhaps reveal some of the veins of the mystery. To do this we should choose a type-centre as it were, and this can be very well represented by the genus *Dendroica*, the species of which probably presents in

its skeleton the characters of our true warblers. Take, for instance, such a well-known skeleton as that of *Dendroica coronata*; it possesses all the typical passerine characters on a small scale, and almost with a provoking likeness to some of the larger forms of the Order. Indeed, could we bring the skeleton of such a Warbler up in size so as to equal the skeleton of *Hesperocichla nævia*, the similitude between them would be marvelously close. As one might easily imagine, the osteological differences between *D. coronata* and such another Warbler as *Protonotaria citrea* are very slight, and the reader has but to compare figures 3 and 15 of the Plates to appreciate the statement I have just made. More than this, I will warrant that from a complete collection of the skeletons of all our American *Passeres*, I can choose representatives from a variety of the families that will intergrade, both as regards size and characters, and connect such forms as our *D. coronata* and *H. nævia*, most perfectly, and I have just said how much the extremes of such a series are alike. Be this as it may, let us return again to the centre of our Warbler system, and speaking quite strictly from osteological premises, we find from *D. coronata* through the genus *Sciurus* the affinity with the *Motacillidæ* is easily demonstrated; no doubt, somewhere in this kinship the Ground Warblers of the genus *Geothlypis* come in. My ideas about the position of *Icteria*, I have already given in my *Chamæa* paper, and I here present a view of the superior aspect of its skull (Fig. 14).<sup>1</sup> Coming back again to the skeleton of our Warbler, how easy is the transition to the Creepers through such a creeping species as *Minotilta varia*, a complete skeleton of which form is before me. The linking with the tanagrine forms I have elsewhere alluded to, and through the genus *Setophaga* perhaps, the clamaratorial group may be linked, and *Vireo* possibly has a kinship here.

Although I have never seen a specimen of the skeleton of the Bahama Honey Creeper (*C. bahamensis*), the sole representative of the next family, the *Cærebidæ*, still I think it is very probable that it should stand precisely where it has been placed in the

<sup>1</sup> Just here I would invite the reader's attention to the protuberance at the posterior extremity of either zygoma in figure 14; they are the anterior ends of the squamosal processes, and not the quadrates, as is the case in figure 1, while in figure 18 a portion of both show.

A. O. U. Check-List; that is, following the Wood Warblers, and at the end of the series which terminates with the Creeping Warblers (*M. varia*). But as I say, this opinion is based solely upon what I have read from other authors upon the topographical anatomy of these birds, and the fact that a similar structure of tongue is common to both Creepers and some of the *Minotiltidæ*.

Arriving next at the Family *Vireonidæ*, we at once enter upon an exceedingly interesting field of research, for the position of the Vireos, for which this family was created to contain, has always been more or less of a mooted question.

Formerly the Vireos were united with the Shrikes (*Laniidæ*), simply from the fact that the bills of certain of the *Vireonidæ* resembled a Butcherbird's, and such names as *Vireolanus* and *Lanivireo* were bestowed upon the subdivisions of the family.

The family *Laniidæ* has now been made to stand next below the Vireos, and here it will be more convenient to deal with these two families together, the more especially as I have already published something in reference to the Shrikes.<sup>1</sup> Now if we choose for comparison the skeleton of such a form as *L. l. excubitorides*, and *V. ludovicianus* from among the Vireos, we see at once that both of these species possess a skeleton exclusive of the skull, that is essentially passerine in all particulars, but with respect to the skull, the most striking differences at once become evident to us, and further show most conclusively the danger of attaching too much weight to a notch in the integumental sheath of the superior osseous mandible, and basing affinities upon it.

*Vireo noveboracensis* (Fig. 16) has a skull which, to all intents and purposes, is but slightly removed from the skull in some of the *Minotiltidæ*. Examining the structures at the base, and critically comparing them one after the other from apex of premaxillary to foramen magnum with the corresponding ones in a skull of *Protonotaria citrea*, we find them to agree almost exactly. Indeed, there appears to be but one noticeable difference; for in the Prothonotary Warbler the posterior external angles of the palatines are pointed, while in the *Vireo* the hinder ends of these bones are obliquely truncated from without inwards, and even in

<sup>1</sup> SHUFELDT, R. W., "Osteology of *Lanius ludovicianus excubitorides*." *Bull. U. S. Geol. and Geog. Surv. of the Terr. Dept. of the Interior*. Vol. VI., No. 2. Washington, Sept. 19, 1881. (Hayden's 12th Annual.)



this latter character it does not agree with the Shrike. Turning to *Lanius*, we meet with a skull wherein all the anterior part of the rhinal chamber is more or less completely filled in with osseous tissue of the cancellous variety; and this so far fills up each external narial opening that there is left on the side of the superior mandible only two small apertures, an anterior subelliptical one, and a posterior vertico-elongated one, just in front of the nasal bone. Where this filling appears externally, it is covered over by a layer of compact bone which is continuous with the outer superficies of the premaxillary and nasals. (See Figs. 100 and 104 of my memoir on the Osteology of *Lanius*.)

The vomer is strictly passerine in this Shrike, but the *maxillo-palatines* are comparatively broad processes and entirely lack the mesial bulbous free extremities, present in *Vireo* and nearly all passerine birds.

*Lanius* has the *inner* posterior angles of its palatines drawn out into conspicuous spine-like processes, and the anterior limb of either of these bones is broad and flat, especially where each merges into the premaxillary.

In all old specimens of these Shrikes that I have ever examined, the palatine ends of the *pterygoids* fuse completely each one with a palatine on its own side,—a very unusual condition,<sup>1</sup> and one never found to obtain in *Vireo*.

Finally, the interorbital septum is far more complete as a rule in Shrikes than it ever is in the Vireos, in which latter it agrees precisely with the Warblers.

The *mandible* of *Lanius* is far more powerfully constructed than we find it to be among the vast majority of *Passeres*, a condition we would very naturally look to be the case.

Speaking strictly from osteological premises, I am of the opinion that *Lanius* is far more closely affined with the Clamatorial birds than it is with *Vireo*; by this I mean that the Vireos are well within the passerine circle, while *Lanius*, also *within* the passerine circle, is close up to its limiting arc, while immediately over this bounding periphery we find the Clamatores, with all their allies, so many of which in other parts of the world possess strong passerine characters in their economy. Compare, for

<sup>1</sup> So firm is this fusion in some skulls that I once macerated a specimen for over six weeks, and yet the pterygoids still remained firmly attached to the palatines, even all sutural traces having completely disappeared.



instance, the skull of a specimen of *Myiarchus crinitus* with the skull of *Lanius l. excubitorides*, and my speculations will at once be appreciated. See how the anterior portion of the rhinal chamber in each is filled in with bone in precisely the same manner; the maxillo-palatines are of the same pattern, as is also the vomer in each, and a number of minor points also corresponding.

Dentirostral bills, like zygodactyle feet and unnotched sterna, are not always sure indications of affinity, as one and all of them may be instances of physiological adaptation, and not indices of fundamental morphological structure determining near kinship. When we come better to know, — and, alas, how deficient our knowledge in such matters yet is, — the anatomy of more of the foreign allies of our Tyrant Flycatchers, and diverging affines of the Shrikes, I am sure the opinion here advanced will not be considered so wide of the mark. Such affinity as the *Laniidæ* may have with the *Corvidæ*, I am not at present prepared to enter upon, as the opportunity to fully examine the material requisite for the decision of such a question has never as yet been offered me.

Last January (1888) Prof. W. Kitchen Parker, F.R.S., kindly defended for me, before the Linnæan Society of London, a paper of mine upon the Morphology of the Macrochires and allied groups of birds. In that paper is given quite an exhaustive account of the skeleton of *Ampelis cedrorum* as a representative of the Family *Ampelidæ*; further, both in text and plates, the family *Hirundinidæ* is very thoroughly dealt with, the structure of every American species being described and compared. Possibly this paper will appear in the course of the year, and in any event it obviates the necessity of my reviewing the morphology of those forms here again. The Swallows constitute a very well-defined family of passerine birds, seeing their nearest allies in the *Cypseli* (Swifts) outside their order; while these latter are in no ways especially affined with the Humming birds (*Trochilī*).

I find also that I will have appear in *The Auk* for October (1888) a paper (illustrated) upon the skeleton of *Habia melanocephala*, wherein the osteology of all our principal species of the Family *Fringillidæ* is carefully presented, so this large and important group will not be touched upon in this paper.

Coming next to the three families of the *Corvidæ*, *Sturnidæ*,

and *Icteridæ*, it will be remembered by those familiar with the writer's memoirs, that they were all treated in a contribution to the *Journal of Anatomy* not long ago,<sup>1</sup> and their affinities pointed out in detail.

Finally, we arrive at the Family *Alaudidæ*, the first one presented at the commencement of the sub-order Oscines in the A. O. U. Check-List, containing as it does the Larks. Here we have two genera, *Alauda* for the single species *A. arvensis*, the skeleton of which I have not before me; and *Otocoris*, with eight species. A number of years ago I published a very full account of the skeleton of *Eremophila alpestris*, in these days more properly described as *Otocoris alpestris arenicola*, and having thus given a complete description of all the details of structure in the osseous system of that species, it will be unnecessary to essay further in that direction.<sup>2</sup> It is very difficult to tell where to place *Otocoris*; I have carefully compared its skull with such genera as *Anthus*, *Molothrus*, *Zonotrichia*, and a variety of others of the *Fringillidæ*, with *Turdidæ* and Tits, and a host of *Passeres*; but passerine as it is itself, it presents cranial characters which seem to be peculiar to its genus. Not the least curious of these is the fusing together, in the adult, of the ends of the sphenotic and squamosal processes, leaving only an elliptical foramen between them, and the latter process being very broad in the transverse direction. Some *Gallinæ* show this feature in their skulls — a fact which we mention in order to explain what is meant. Newton has said, "There is, however, abundant evidence of the susceptibility of the Alaudine structure to modification from external circumstances — in other words, of its plasticity; and perhaps no homogeneous group of *Passeres* could be found which better displays the working of 'natural selection.' " And again, in the same place, "Almost every character that among passerine birds is counted most sure is in the Larks found subject to modification. The form of the bill varies in an extraordinary degree"; from which

<sup>1</sup> SHUFELDT, R. W., "On the skeleton in the genus *Sturnella*, with osteological notes upon other North American *Icteridæ*, and the *Corvidæ*." *Jour. of Anat. and Phys.*, Vol. XXII. (n.s. Vol. II.), pp. 309-350. London, April, 1888. Plates XIV., XV.

<sup>2</sup> SHUFELDT, R. W., "Osteology of *Eremophila alpestris*." *Bull. U. S. Geol. and Geog. Surv. of the Terr. Dept. of the Interior*. Vol. VI., No. 1. Washington, D.C., Feb. 11, 1881.

point this distinguished ornithologist and anatomist cites numerous species of Larks with bills in some as slender as a Warbler's, to such a species as *Rhamphocorys*, where "it is exaggerated to an extent that surpasses almost any Fringilline form."<sup>1</sup>

I am inclined to think that we have no birds in our avifauna to which *Otocoris* is especially closely related, and that as a species it has arisen from some Old World stock, and only secondarily spread to this continent at a comparatively recent epoch. As will be observed from the figures in my memoirs, quoted above, the structures at the base of the skull in *Otocoris* are strictly passerine in their arrangement; quite similar, for instance, as we find them in *Anthus*, but by no means so delicately constructed; rather the reverse, we should say.

In figures 22, 23, and 25 of the Plates to the present memoir I present views of the superior aspects of the skull from specimens of *Habia melanocephala*, *Cyanocephalus cyanocephalus*, and *Piranga ludovicianus*, respectively; these drawings were made by me and here offered to the end that they might be compared with similar views of the skulls of other passerine birds, which have likewise been presented in the Plates, but described more in detail in the text; the three foregoing species mentioned belonging to forms which I have described in papers in the hands of my publishers, but not yet in print, and in other memoirs. Especial attention is invited to the form and marked capacity of the brain case in the Piñon Jay (Fig. 23), one of the *Corvidæ*, as compared with similar parts in such forms as the Tyrant Flycatchers (Figs. 18 and 19), or even such strictly passerine types as some of the Thrushes and Warblers (Figs. 4 and 5). Then again, compare this feature in such a true Thrush as *Myadestes* with a Titmouse, as shown in figures 1 and 9 respectively. Further on in my final recapitulation it will be my aim to attempt to point out if possible the probable significance of such an evident character as this, and in the foregoing paragraphs I have already strongly hinted as to what my interpretation of it may be. That it is incontestable evidence of a perfection of organization in any vertebrate form, all the truths of paleontology, physiology, and recent investigations in morphology, go to sustain.

But we will have nothing more to do with the osteology of the

<sup>1</sup> NEWTON, A., *Encyc. Brit.*, Art. "Lark." Vol. XIV., p. 316 (9th ed.).



*Oscines* in this place, deferring all such questions to the closing arguments of this paper, in the "Conclusions," where they more properly belong, and now at once proceed to the consideration of the skeleton in our American clamatorial birds, of which there are some thirty-six species and sub-species in our United States avifauna.

By referring to the scheme of the families as given at the commencement of this paper, it will be seen that the clamatorial family, the *Tyrannidæ*, about to be considered, occupies the first position in the list, which there means that it is of the lower, indeed lowest, group of passerine birds, so far as we are enabled to judge from their structure.

Coues in characterizing this family has said that it is peculiar to America, and is "one of the most extensive and characteristic groups of its grade in the New World, the *Tanagridæ* and *Trochilidæ* alone approaching it in these respects. There are over 400 current species, distributed among about 100 genera and sub-genera. As well as I can judge at present, at least two-thirds of the species are valid, or very strongly marked geographical races, the remainder being about equally divided between slight varieties and mere synonyms. Only a small fragment of the family is represented within our limits, giving but a vague idea of the numerous and singularly diversified forms abounding in tropical America. Some of these grade so closely toward other families, that a strict definition of the *Tyrannidæ* becomes extremely difficult; and I am not prepared to offer a satisfactory diagnosis of the whole group" (*Key*, 2d ed., p. 428). For the manner in which the family has been classified by our avian systematists, the reader is once more referred to the A. O. U. Check-List. The material at present at my hand, some of which I am greatly indebted to Mr. H. K. Coale of Chicago for, by which I hope to pass in review the skeletology of the *Tyrannidæ*, comes mainly from the genera *Tyrannus*, *Myiarchus*, *Sayorius* (all three species), *Contopus*, and *Empidonax*. Figures 18 to 21 inclusive, of the Plates, illustrate skulls and other bones of these birds; and when speaking above of the craniology of *Lanius*, I dwelt to some extent upon certain features which characterize the skull of *Myiarchus*. As a rule in these *Tyrannidæ*, the brain-case is comparatively small and the sides and vault of the cranium rounded. Relatively, the



brain-case seems to be larger in such a species as *T. tyrannus* than it is in some of the other genera. This feature in them all, however, is made to be still more apparent by their great, wide, and flat superior osseous mandibles, which constitute such a striking character in the skulls of the vast majority of these Tyrant Flycatchers. When we come to examine the bony, upper beak, in such a form, for instance, as the King-bird (*T. tyrannus*), we find that the external narial apertures are large and sub-elliptical in outline, and these, when covered by the thinner posterior part of the horny sheath of the mandible, constitute the nasal fossæ of descriptive ornithologists. It is in the extreme fore part of either of these that the small subcircular and functional nostril opens, while in some species, or certain individuals of some species, nearly all this anterior part of the rhinal chamber may fill in with bone, in a manner I have already described above. A slit, on either side, just in front of the nasal bone, remains open (but is always covered with the integumental mandibular sheath), and the aforesaid aperture comes to be the true outer nostril. In figure 19 I show this condition in a specimen of *M. crinitus*, but in another skull before me of *M. cinerascens*, very little bone is deposited in these parts, they being more like the skull of the Black Phoebe shown in figure 18. All grades of this condition are to be met with between these two extremes. Sometimes a small, curled piece of bone remains free, on either side, within the rhinal chamber, and, held in place by surrounding structures, resembles a "turbinal bone"; and in addition to these, the *lacrymals* remain free in these clamatorial birds, being situated, in each case, immediately anterior to the *pars plana*. These I have figured for *M. crinitus* in my paper on the Macrochires, in the hands of the Linnæan Society of London.

Flat, and for the most part smooth, the under side of the premaxillary region of the skull in front is bridged across with a thin, bony layer, a condition rarely found among our oscine passerine birds, except in such species as *Setophaga*.

Tyrant Flycatchers, as a rule, have the interorbital septum far more perfectly completed in bone than do either the Warblers or Thrushes, or the nearest allies of these latter; and in *M. cinerascens* a large foramen exists between the mesethmoid and the *pars plana*, immediately beneath the frontal region of the

skull. The *vomer* is fashioned much as we find it among the average oscines, but the *maxillo-palatines* always depart in their pattern from those birds, for they are broad where they come away from the maxillaries, and gradually taper to their free mesial ends, which are never finished off by a bulbous extremity, such as we find in *Harporhynchus*, for instance, though I have found in *Myiarchus* the points of the *maxillo-palatines* bent backwards, thus simulating the condition referred to in the more highly organized *Passeres*. We usually find, too, a foraminal opening piercing the base of either *maxillo-palatine* in the Clamatores, a feature especially conspicuous among the larger American species, though commonly present in a more or less marked degree in them all.

The interior of the cranial casket seems to offer us no very good characters which can be utilized, either in classification, or in any way, beyond the question of relative capacity, point to the affinities of the several groups under consideration.

These Tyrant birds always seem to have the sclerotal plates of the eyeballs very narrow, and in old specimens these show an evident tendency to fuse together, and in a specimen of *Sayornis nigricans* at my hand this has actually taken place. Nothing peculiar characterizes either the hyoidean apparatus or the ossicles of the ears. The *mandible* is not much stronger, in comparison with the size of the various species, than we find it among birds of an equal size in the oscine group; and in *Lanius* it is much the stronger. *Myiarchus cinerascens*, for example, has the symphysis to its mandible wide, shallow, and yet rather deep in the antero-posterior diameter; the rami are narrow in the vertical direction, the vacuities small, and the articular cups and processes respectively shallow and feebly developed.

It will be seen from this brief description that very excellent differential characters distinguish the skulls of typical oscine and clamatorial birds. Not so, however, with the remainder of the axial skeleton, nor with the appendicular skeleton; for in all the *Tyrannidæ* examined by me I find the vertebral column and ribs arranged upon the same plan as in the vast majority of the oscines, with shoulder girdle, sternum, and pelvis of the same general pattern. One thing must be nevertheless noted, and that is, that the skeleton is far more pneumatic among the Clamatores than it is usually found to be in the Oscines,—

the humerus (and sometimes the femur?) is always pneumatic, and in *Myiarchus* a single row of quite sizable foramina extend the entire length of the middle line of the sternum adown its thoracic aspect. I am inclined to think, too, that other long bones in the skeleton of this species have the air admitted to the cavity of their shafts; but here I judge only from appearances; for if the foramina be present, I failed to find them, even with the aid of a good lens, in some cases.

With this succinct account of the osteology of some of the genera of our American *Tyrannidæ*, I will close the general descriptive part of my memoir, and pass to my conclusions, based, as these latter will be, upon the facts herein brought out. In this place, however, I would like to add that I am aware that I have not touched upon the embryology of any of the species treated, nor was that my aim originally. The paper proposes nothing further than a general description of the skeleton in adult forms, and such deductions as we may logically make upon the comparison of such data. No doubt when we come to critically consider the embryology of many of the species, and draw more elaborate comparisons, a great deal of additional information will be gotten at, and some of the more complex questions in affinities by such means be decided. Especially will this be true in the case of comparing the embryos of *Tyrannidæ* with those of the *Laniidæ* and *Setophaga* and others.

The most I can hope for the present effort, is to establish broad lines in the osteology of the *Passeres* of this country, and present a framework, as it were, which may serve as a basis upon which may be reared in the future those refinements in avian morphology, that forever tend to shed a more certain light upon all vexed questions in the taxonomy of this perplexing Class.

#### CONCLUSIONS.

For fully ten years past and more, the writer has busied himself with the anatomy of the passerine birds of this country, during which time he has also read many of the works of others upon the same subject; so then, although this memoir deals alone with the osteology of the order *Passeres*, it is very likely that now we come to sum up our knowledge in these fields, and draw our conclusions, and offer our opinions as to classification and affinities, — it is very likely, I say, that we will not be en-

tirely governed in such matters by osteology alone, but will be more or less influenced by other considerations, such as our knowledge of the habits, range, nidification, anatomy of the various systems, plumage of young, and general morphology of the species dealt with.

At the commencement of the present paper, I gave a list of the passerine families arranged in the order given in the A. O. U. Check-List, starting in with the *Tyrannidæ*, and ending with the *Turdidæ*, the first supposing to represent the least specialized types in their organized structure, and the last the highest. Now I will here give a scheme of the same families, rearranged in accordance with the facts sent forth above, and other data in our possession, and follow this rearrangement by a few words in its defence.

ORDER.	SUB-ORDERS.	FAMILIES.
	Clamatores . .	1. Tyrannidæ.
		2. Laniidæ.
		3. Ampelidæ.
		4. Hirundinidæ.
		5. Alaudidæ.
		6. Certhiidæ.
		7. Vireonidæ.
		8. Motacillidæ.
		9. Sylviidæ.
		10. Cœrebidæ.
PASSERES . .	Oscines . . . .	11. Mniotiltidæ.
		12. Cinclidæ.
		13. Troglodytidæ.
		14. Turdidæ.
		15. Paridæ.
		16. Tanagridæ.
		17. Fringillidæ.
		18. Icteridæ.
		19. Sturnidæ.
		20. Corvidæ.

Professor Alfred Newton, F.R.S., has advanced very cogent reasons for placing the *Corvidæ* at the head of the *Passeres*, already cited above, and the present writer fully coincides in his opinion, and further believes with that eminent authority, that the Raven should lead the family. *Corvus corax* has a skeleton of the highest type of oscine organization, a statement that



applies with equal force to much else in its economy; its brain is relatively larger, in proportion to the size of the bird, than others of the order; its young substantially have the plumage of the parents at a time when as nestlings they first take on their plumage; and finally, the Raven is a far more intelligent bird than any species of *Sialia* that the author has ever made a psychological study of, and, indeed, than any other Thrush. The power of song is by no means an index of a high order of intelligence, much less an indication of a highly specialized organization.

Through their natural structural affinities, the *Corvidæ* must next be followed by the *Sturnidæ* and *Icteridæ*, and through such linking species as *Molothrus* and *Dolichonyx* these must be followed by the *Fringillidæ*, whereas no family can stand between these latter and the *Tanagridæ*. Admitting then that the *Corvidæ* are fully entitled to stand at the head of the Order *Passerines*, and that the Starlings, Orioles, Finches, and Tanagers follow as a natural series or sequence, I am fully convinced that the *Paridæ* should, by all our previous arguments, enjoy the next position of distinction. Indeed, were it not totally out of the question to introduce a family *in among* the first five I have placed first in the list, the *Paridæ* might hold a more exalted rank, for in my opinion the group of Tits and their more immediate affines are birds of markedly high organization. They possess unusually large brains for their size; there is just a possibility that they are connected with the *Corvidæ* through such a species as *Perisoreus*; they show wonderful ingenuity in the construction of their nests; the plumage of the young is almost identical with the parents; and finally, some of their kin (as *Chamæa*) have absolute scutellate *podothecæ*.

As to this last character, referring as I do to the "booted" tarsus, or a tarsus which shows in the adult a continuous podothecal envelop, granting that it is an indication of high specialization of structure in birds, I am in no way prepared to say that it is to be outweighed by a relatively larger brain for any particular species. The size of the brain in my judgment, as compared with the size of its owner, being by far the better criterion of perfection in general specialized structure. Perhaps the "booted tarsus," and such a degree of refinement in structure as we find in the turdine syrinx, may be claimed to be on a par.

There is another character of no inconsiderable importance, and may perhaps be entitled to greater weight than the booted tarsus, and that is the reduction of the *ten primaries* of the wing to *nine*. The Tanagers show this feature, and it is a good one to hold them in the place which I have assigned them; moreover, it gives them precedence over the more lowly organized *Turdidæ*, which in reality should long ago have been recognized.

Few, however, will question the claim of the *Turdidæ* to the next place in the series, and it is there that they have been placed in my scheme. High organization in them is seen in some of the species having relatively rather large brains; in the booted tarsi of some of the species; in the syrinx; in the *Turdinæ* possessing a spurious first quill; and some few other minor points. Evidences of their being structurally and psychologically lower in the scale are seen in their young having a first plumage which in all cases is different from the plumage of the adult; in some of their near affines having comparatively small brains; in none of them showing a marked degree of intelligence; finally, in some of their near kin being aberrant forms of rather a low order of organization, as *Oroscoptes*.

Structurally linked with the *Turdidæ*, we have the *Troglodytidæ*, their nearest affines in our avifauna, and I have ranked them next in my series. Following these I have placed the *Cinclidæ*, as *Cinclus* undoubtedly has strong turdine affinities, and perhaps some kinship with the Wrens.

Below the *Cinclidæ* I have placed our family of Wood Warblers (*Minotiltidæ*), containing as it does such thrush-like forms as are found in the genus *Sciurus*, which, osteologically at least, appear to be related to *Cinclus*. In this group *Setophaga* demands a far more careful examination than it thus far has ever received, and I believe it was McGillivray who threw a shade of suspicion over its morphology by saying that its syrinx was very much the same as we find it in the Clamatores. At present I have only an imperfect skull of a Redstart before me (*S. ruticilla*), and have met with none of this genus for several years past. From such a genus as *Minotilta* of the *Minotiltidæ*, we pass naturally to the *Cærebidæ*, and I have allowed them to stand next in my series. These latter are followed next below by the *Sylviidæ*, containing such forms as the Kinglets and Gnatcatchers, birds that, although in the former the tarsus is booted,

and the first quill of the wing spurious, are birds of relatively very small brains, and the young males in *Regulus calendula*, at least, do not take on the plumage of maturity until the second year. Good, strong, sub-family lines must be recognized as being drawn between the *Regulinæ* and the *Poliophtilinæ*.

From the last three-mentioned families in my serial arrangement, we pass naturally to such groups as the *Motacillidæ* and *Vireonidæ*; the former being hardly anything more than terrestrial *Sylvias*, and the latter, judging from their skeletons, have closer affinities with the Warblers than with any other family which we have thus far investigated. After these the true Creepers (*Certhiidæ*) have been placed, forms which, osteologically and otherwise, have no especial claim to be ranked with birds of undoubtedly higher organization. This remark applies with equal force to the *Alaudidæ*; indeed, still more pointedly to them, for the Larks in addition have an anomalous structure of the tarsal thecæ, and one from its double scutellation of perhaps a lower type organization. In them, too, the young have a different plumage from the parents.

For a long time I was at a loss to know where to place the Swallows (*Hirundinidæ*), and they have been crowded to near the foot of the list, not that they have not a few points in their economy indicative of a certain degree of rather high specialization; still, although truly passerine birds, they are birds of comparatively small brains, and their young differ in their plumages from the parents; and, while we do not yet know the exact affinities of the *Hirundinidæ*, all the speculations in that quarter have been in the direction of associating them with groups of recognized low type of organization.

Newton says of them: "But altogether the family forms one of the most circumscribed, and therefore one of the most natural groups of *Oscines*, having no near allies; for, although in outward appearance and in some habits the Swallows bear a considerable resemblance to Swifts, the latter belong to a very different order, and are not passerine birds at all, as their structure, both internal and external, proves. It has been sometimes stated that the *Hirundinidæ* have their nearest relations in the Flycatchers; but the assertion is very questionable, and the supposition that they are allied to the *Ampelidæ*, though possibly better founded, has not as yet been confirmed by any anatomical



investigation. An affinity to the Indian and Australian *Artamus* (the species of which genus are often known as Wood-Swallows, or Swallow-Shrikes), has also been suggested; and it may turn out that this genus, with its neighbors, may be the direct and less modified descendants of a generalized type, whence the *Hirundinidæ* have diverged; but at present it would seem as if the suggestion originated only in the similarity of certain habits, such as swift flight and the capacity of uninterruptedly taking and swallowing insect-food on the wing." (A. N., *Brit. Encyc.*, 9th ed., Vol. XXII., p. 730.)

Huxley has said "the *Cypselidæ* are very closely related to the Swallows among the Coracomorphæ" (*P. Z. S.*, 1867, p. 469); which is equivalent to my having substantially said, in another connection, that the *Cypseli* are but profoundly modified Swallows, which latter are their nearest affines among the *Passeres*. So taking it all and all, I am at present inclined to believe that the Swallows represent rather a low type of organization among the passerine birds.

The *Ampelidæ*, which I have placed even lower in the scale than the *Hirundinidæ*, show in their organization all, or nearly all, those features which, as we now interpret them, are indications of an inferior grade of avian organization. All of these characteristics I have elsewhere fully dwelt upon and pointed out in detail.

In the body of the present memoir, the writer entered quite largely upon the question, as to the reasons for assigning the *Laniidæ* a low place in the passerine order, and it will be unnecessary to take up that part of our subject here again. I am of the opinion that they are as low, if not the lowest type of bird-structure we have in our United States avifauna, among the *Oscines*.

The classification of our sub-order of clamatorial birds, as represented by the *Tyrannidæ*, requires no especial comment from me, in this place; it has been left in the same position it occupies in the A. O. U. Check-List, and probably meets with the views of the majority of ornithotomists, as well as the systematists the world over. It seems, I think, fully supported by all that we at present know of their economy.



NOTE. — With the exception of figures 24 and 26, all the drawings in the Plates are of the size of life; the excepted figures being twice the natural size. They were all drawn by the author directly from specimens in his own cabinet, with the exception of the skull of *Sitta c. aculeata*, which belongs to my son (Fig. 16). The skeleton of *Ampelis cedrorum* was presented me by Mr. H. K. Coale of Chicago, and the *Sayornis nigricans* by C. A. Allen of Nicasio, California; while the Smithsonian Institution generously furnished the specimen of the Varied Thrush (*H. navia*), shown in figures 3 and 26. All the others, with a few exceptions, were collected by the author in various parts of the United States, as Wyoming, New Mexico, Louisiana, and elsewhere.

#### EXPLANATION OF PLATE V.

- FIG. 1. Superior view of the skull of *Myadestes townsendii*; ad. ♂, New Mexico.  
 FIG. 2. Superior view of the skull of *Merula migratoria propinqua*; ad. ♂.  
 FIG. 3. Superior view of the skull of *Hesperocichla navia*, ad. ♂. (No. 81, 166. S. I. Col.).  
 FIG. 4. Superior view of the skull of *Turdus a. pallasii*; adult.  
 FIG. 5. Superior view of the skull of *Polioptila cerulea*, ad. ♀, New Orleans, La.  
 FIG. 6. Superior view of the skull of a specimen of *Regulus satrapa*, ad. ♂, collected by Mr. H. K. Coale at Hartford, Conn.  
 FIG. 7. Superior view of the skull of *Psaltiriparus plumbeus*, ad. ♂, New Mexico. (Probably one of the very smallest passerine skulls of existing birds.)  
 FIG. 8. Superior view of the skull of *Chamaea fasciata henshawii*; from a specimen collected in California by Mr. F. Stephens.  
 FIG. 9. Superior view of the skull of *Parus inornatus griseus*; ad. ♂, New Mexico.  
 FIG. 10. Superior view of the skull of an adult specimen of *Parus gambeli*.  
 FIG. 11. Superior view of the skull of *Sitta c. aculeata*.  
 FIG. 12. Superior view of the skull of an adult ♀ specimen of *Troglodytes aëdon parkmanii*.  
 FIG. 13. Superior view of the skull of *Anthus pensilvanicus*; adult.  
 FIG. 14. Superior view of the skull of a ♂ specimen of an adult *Icteria v. longicauda*, collected by the author at Fort Wingate, New Mexico.  
 FIG. 15. Superior view of the skull of the Prothonotary Warbler (*Protonotaria citrea*); ad. ♂, New Orleans, La.  
 FIG. 16. Superior view of the skull of *Vireo noveboracensis*; adult.  
 FIG. 17. Superior view of the skull of *Ampelis cedrorum*; adult.  
 FIG. 18. Superior view of the skull of *Sayornis nigricans*.

Fig 1.



Fig 2.



Fig 3.



Fig 4.



Fig 5.



Fig 6.



Fig 7.



Fig 8.



Fig 9.



Fig 10.



Fig 11.



Fig 12.



Fig 13.



Fig 14.



Fig 15.



Fig 16.



Fig 17.



Fig 18.



R. W. S. Gould del. and engr. do.







## EXPLANATION OF PLATE VI.

FIG. 19. Superior view of the skull of *Myiarchus crinitus*; adult.

FIG. 20. Anterior aspect of the sternum of *Myiarchus crinitus*.

FIG. 21. Dorsal aspect of the pelvis of *Myiarchus crinitus*; the bones figured in this and figure 20 are from the same skeleton which furnished the skull shown in figure 19.

FIG. 22. Superior view of the skull of an adult ♂ specimen of *Habia melanocephala*; New Mexico.

FIG. 23. Superior view of the skull of *Cyanocephalus cyanocephalus*; adult.

FIG. 24. Right lateral view of the skull of *Myadestes townsendii*, ad. ♂;  $\times 2$ .

FIG. 25. Superior view of the skull of a specimen of *Piranga ludovicianus*; adult.

FIG. 26. Right lateral view of the skull of an adult specimen of *Hesperocichla naevia*;  $\times 2$ .

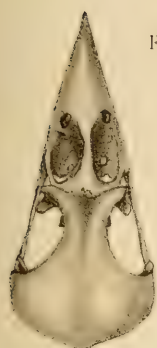


Fig. 19

Fig. 20



Fig. 21

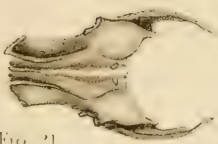


Fig. 22



Fig. 23

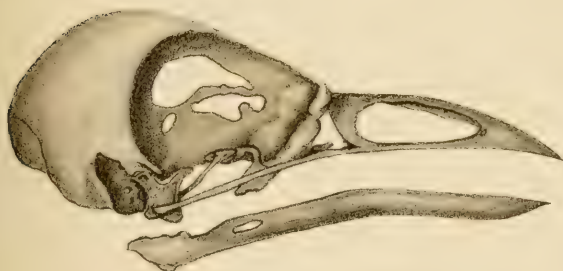


Fig. 24



Fig. 25

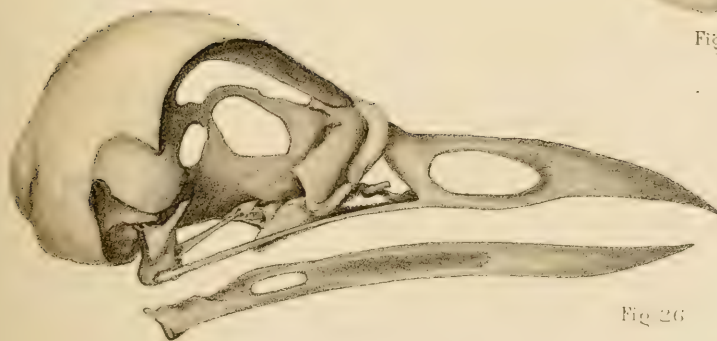


Fig. 26

R. W. Shufeldt, del. and col.



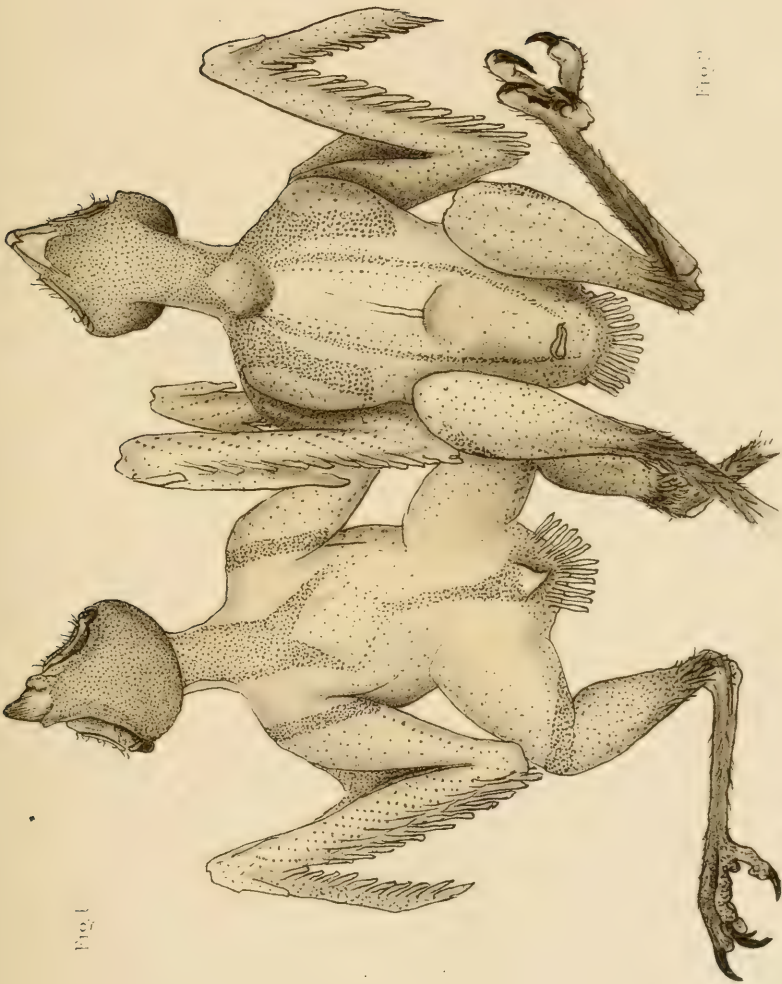


Fig. 1

Fig. 2

SPEOTYTO CUNICULARIA HYPOGAEA.  
NAT. SIZE.

REV. EDWARD ADAMS, F.R.S.  
LONDON: H. K. MUMFORD, 1874.





## NOTES ON THE ANATOMY OF *SPEOTYTO* *CUNICULARIA HYPOGÆA*.

R. W. SHUFELDT, M.D., C.M.Z.S.

AMONG my alcoholic birds that I collected in Arizona and New Mexico, during the years of 1884 to 1888 inclusive, I find two very fine specimens of the Burrowing or Prairie Owl (*Speotyto*), and, as there are certain parts of the anatomy of this remarkable species, so far as the writer is aware, which have not as yet received the attention of the ornithotomist, it will be my aim in the present contribution to offer a few remarks upon the subject. Naturalists are quite familiar with the two species of this owl and their geographical ranges; their habits and nidification; and something of their external or topographical anatomy; so these chapters in their life-history need nothing from me here.

### THE PTERYLOGRAPHY.

Upon plucking a specimen of *speotyto*, we find that it possesses *twenty-five* remiges, and *twelve* rectrices. These numbers, it would seem, agree with the majority of the *Striges*; but in the remainder of its pterylography, *Speotyto* exhibits some marked departures from the patterns laid down for this order by so eminent an authority in such matters as Nitzsch.<sup>1</sup> The Burrowing Owl, however, agrees in possessing *feathers without an aftershaft, and a tuftless oil-gland*, points which essentially distinguish this group pterylographically. Differing from both *Strix bubo* and *Hybris flamea*, as drawn by Nitzsch, *Speotyto* has its head completely feathered, crown, occiput, sides and throat; and, furthermore, the anterior and posterior cervical tracts are notably broad, which is contrary to the rule in these nocturnal rapacious birds, according to the writer just quoted (see Figs. 1 and 2 of the Plate). About the middle of the neck, the anterior cervical tract bifurcates, each bifurcation passing down to

<sup>1</sup> *Pterylography*, Nitzsch, C. L. (Dr. Sclater's translation; Ray Society edition, Lond. 1867). pp. 67-71, *Taf.* II., Figs. 8-11.

merge with the anterior parts of the continuous humeral and ventral tracts at the shoulder. A few feathers are also found at the hinder part of the fossa between the limbs of the *os furcula*. The *ventral tract* is divided; the inner branch being long and narrow, composed, as it is, of only two rows of contour feathers. Either row passes almost in a direct line to the outer margin of the vent on the same side, being strictly defined for the lower moiety of its course; more diffuse above. On the other hand, the external branch is very broad, and strongly marked, as shown in Fig. 2, — its postero-external angle throwing upwards towards the shoulder “a hook” of large contour feathers; the area at the outer aspect of the breast between this latter line and the external branch of the ventral tract is diffusely feathered with a number of large feathers.

Nitzsch evidently had a specimen of the present species (*op. cit.* p. 70), but I am very much inclined to believe that it was in poor condition, from what he says about it, and the next form he describes (*Strix pygmæa*); probably in moult, and kept too long besides. In any event he failed to note the characters I have just given for the pterylæ of the ventral aspect of this owl's body. Anteriorly the legs are pretty well feathered, and sparsely distributed down-like feathers of no great size cover the tarsi in front, and become exceeding small as they pass to the toes on their upper surfaces. It is said that the shanks are more extensively denuded in the Floridan form of the Burrowing Owl.<sup>1</sup>

Our subject has its “alar tracts” strongly marked, the feathers being regularly disposed on their dorsal aspects, consisting of a row of four or five feathers running from each quill in the direction of the patagium.

Dorsally, the spinal tract shows a conspicuous fork at a point between the shoulders, as shown in Figure 1 of the Plate, and a single and more feeble row of feathers connect the apex of either limb of this bifurcation, with the hinder part of the spinal tract where it begins again, in the middle line. From this latter point, it grows stronger and broader once more, and upon approaching the large papilla of the uropygeal gland, it surrounds that structure; the caudal region between it and the rectrices being well feathered.

<sup>1</sup> COUES, E., *Key to North American Birds*, 2d ed., p. 517. (*S. c. floridana*.)

Strong "crural" and "humeral" tracts characterize the pterylography of *Speotyto*, the feathers of the latter being very long and large. The femoral pterylæ are fairly well pronounced in this owl, and a few scattered feathers may occur beyond it, as do a few between the limbs of the bifurcation of the spinal tract, though these latter are inclined to be of the downy variety.

This description goes to show, then, that *Speotyto* has a pterylography, in some particulars, quite its own, though it is possible that it may largely agree with such genera in this respect, as *Glaucidium* and *Micrathene*, but I have not specimens of these at my hand at present, wherewith to compare it. *Speotyto* has no ear-valve, and a few delicate feathers are distributed over the eyelids. As compared with the species of owls described by Nitzsch, its pterylography is peculiar in the marked and unusual breadth of the tracts, and in that the head is completely covered with feathers upon all its aspects.

#### ON CERTAIN STRUCTURES OF THE HEAD.

Seven or eight years ago the writer published a detailed account of the skeleton of the Owl we now have under consideration, so that we will not be required to touch upon that part of its anatomy here, or only in so far as some special point seems to demand it (*U. S. Geol. and Geogr. Survey of the Terr. Dep't of the Interior*. Hayden's 12th Ann., pp. 593-626, 3 pls.). Upon removing the teguments of the head, we are to note that the moderately large eyes of *Speotyto* look forwards and outwards, but do not project as prominently as we find them sometimes in other *Strigidæ*. The nictating membrane is attached in the usual manner to the antero-superior part of the eyeball, which latter possesses a deep encasement of sclerotal plates. As in most Owls, the frontal region of the cranium is narrow, and the *supraorbital processes* are spiculiform, projecting backwards and a little outwards; to the inner side and apex of either of these, and to the entire posterior orbital margin, is attached a dense, fibrous membrane, which covers the globe of the eye posteriorly, being inserted finally to the cranium in front of the ear, to the zygoma slightly, and to the under side of the eyeball, upon which, throughout its extent, it is drawn tightly down.



In front of the orbital cavity is a spongy bone of some size, which I described in my memoir upon the osteology of *Speotyto* as the *lacrymal*, and I still take it to be such, and believe the processes above referred to as the supraorbital processes, to be developments on the part of the frontal bones. Two skeletons of nestlings of *Bubo virginianus* seem to indicate this: specimens kindly collected for me by Dr. W. S. Strode of Bernadotte, Ill.; though in these, these processes are exceedingly small. Among certain Hawks and Falcons the arrangement is very different; for in such a species as *Falco sparverius*, for example, these processes are very long and conspicuous; but they are here the true lacrymals, and send down a descending process, which, in either one, reaches to the maxillary, and articulates with the entire outer margin of the *pars plana*. In this little Falcon no such bone exists as the lacrymal which I have described for *Speotyto*, its place being monopolized by this descending limb of the very differently constructed lacrymal in it, and to which I have just alluded. In such characters as these, then, we find truly a great difference between such species as our Burrowing Owl and the Sparrow Hawk.

Removing the vault of the cranium, and breaking down the walls of the brain-case, here composed of very delicate tables and abundant open diploëic tissue, we find the brain of a form common to many *Strigidaë*,—the cerebral hemispheres large, smooth, and somewhat pear-shaped, mounting as they do considerably above the rather small cerebellum. The pineal body is of no great size, while the optic lobes, as well as the optic tracts, are situated in the deep excavation formed at the bottom of the cranial casket. All the cerebral nerves, including the first pair, are of mere thread-like proportions, as soon as they are given off from the brain mass; and, indeed, the medulla oblongata is of small calibre compared with the size of the bird.

An interesting feature is seen at the side of the skull in *Speotyto*, where the tendon of the temporal muscle passes through a foramen, above the squamosal, on the way to its insertion upon the mandible. This arrangement does not exist in such species as *Asio wilsonianus* nor *Syrnium nebulosum*; the former of these, with a very different skull from the Burrowing Owl, has simply a minute notch devoted to the same purpose;

while in *Syrnium*, with another very dissimilar pattern of skull, this is shown in a deep groove.

The eyes of *Speotyto* present nothing worthy of special note, beyond what we know of these organs among the Owls generally. We observe, that the optic nerve is of rather small calibre, for a strigidine bird, while this species affords an excellent type upon which to study the special musculature of the eye, and the ever interesting arrangement of the pyramidalis and its tendon.

This specimen has no *vomer*, its place being superseded by a median sheet of dense fibrous membrane; and I am strongly inclined to believe that this bone never ossifies in *Speotyto*. A skull of *Syrnium* at my hand also lacks this element, while in *Asio wilsonianus* it is very small, and of peculiar construction, being sharply pointed in front, hollow, and light, and delicate throughout. *Falconidæ* usually always have a good-sized vomer, but from what has just been said, we must believe that this is the exception in the Owls.

Nothing peculiar seems to characterize the internal ear, which I carefully examined; nor the tongue, nor the upper larynx.

#### THE PECTORAL MUSCLES.

For a bird that so seldom seems to resort to flight of any great extent, *Speotyto* has its pectoral system of muscles very well developed.

The *pectoralis major*, although not very thick, as the sternal keel is inclined to be shallow, makes up in width, and on the whole would be considered rather a powerful muscle. It exhibits the usual origin and insertion, completely covering the next two to be noticed.

Of these the *pectoralis secundus* is also of quite a considerable bulk, arising from its most usual site on the anterior aspect of the sternal body, and carina, it shows the bipenniform structure for which it is notorious, and its tendon passes up through the tendinal canal, formed by the bones of the shoulder girdle, to be inserted into the humerus after the common fashion as seen among birds generally.

A *pectoralis tertius* of no mean dimensions, but presenting nothing peculiar, is also found in this Owl, and it completely covers, in my specimen, the row of sternal articulations of the hæmapophyses of either side.

## CERTAIN MUSCLES OF THE FOREARM AND THIGH.

Professor Garrod has already pointed out that the *expansor secundariorum* muscle is absent in the *Strigidae* (*Coll. Sci. Mem.*, p. 329), and I find *Speotyto* to be no exception to the rule. On the other hand, the patagial muscles of this family are not alluded to by him, and here offer several points of interest; for although the origin and insertion of the *tensor patagii longus* are as we find them in nearly all ordinary birds, the same cannot be said of the *tensor patagii brevis*. This latter has its carneous portion at the shoulder much as we always find it, while its slender tendon in descending for insertion upon the *extensor metacarpi radialis longus* of the antibrachium, bifurcates at about the middle of its course,—the inner or proximal slip attaching itself as usual to the tendon of the aforesaid extensor of the forearm, and from the point of its insertion a tendon passes by a gentle curve over the outer aspect of the muscles of the antibrachium, towards the wrist, and gradually approaches the ends of the quills of the secondary feathers, into which it finally becomes inserted at a point about opposite the site of the middle and distal thirds of the ulna. To return to the remaining slip, the anterior one, of the bifurcated tendon of the *tensor patagii brevis*, it too becomes inserted into the tendon of the *extensor metacarpi radialis longus* at a point situated about half a centimetre beyond the insertion of the proximal slip, and in the same line. It will be interesting to compare this arrangement of the short tensor of the patagium in other *Strigidae*, as well as in Raptorial birds generally. Before writing out this account of it I very carefully examined the muscles in question in both limbs, and found them to agree exactly.

*Speotyto* lacks the *biceps slip to the patagium*, as seems to be the case in all Owls.

Passing to the muscles of the thigh, we find the femoro-caudal present, and for a representative of this family, rather large; the ambiens, the tensor fasciæ, the semitendinosus and its accessory slip, and the accessory femoro-caudal are all absent. This arrangement agrees with the several species of Owls examined by Garrod, though that distinguished ornithotomist did not apparently examine the present bird, while he did investigate this point in at least three forms of *Athene*.



Incidentally, I may remark here, that in *Speotyto* the main nerve of the leg is the sciatic; the main artery, the sciatic artery; and the main vein, the femoral.

Nowhere in Garrod's work do I find a place where he paid any especial attention to the arrangement of the plantar tendons in the Owls, and he seems to have let this matter rest with his investigation of four or five species of diurnal Raptores; and of these he says that "the *flexor longus hallucis* divides into two moieties opposite the lower end of the tarso-metatarsus, one of which runs to the hallux. The other part is the representative of the vinculum of the above-mentioned birds; it is peculiar, however, in that, instead of joining the tendon of the *flexor perforans digitorum*, before it is distributed to the anterior toes, it mostly runs down to blend with the slip which is associated with the inner of these (digit 2) only [figures it for *Tinnunculus alaudarius*]."

"In *Geranoëtus aguiæ* and in *Polyborus*, besides the special tendon from the hallux-muscle to the second digit, there is a broad, thin vinculum present, as in *Gallus*. In the Accipitres Diurnæ, the arrangement of the tendons, therefore, differs in different groups—in *Baza* their distribution being quite normal, that is, as in the first described; in *Polyborus*, *Haliaëtus*, *Tinnunculus*, and *Geranoëtus*, this condition is combined with a special tendon to the second digit, which greatly increases its power of flexion." (*Coll. Sci. Mem.*, pp. 293, 294.)

Now of the *Cathartidæ*, he further adds, in the same place, that, "the two deep flexors descend beyond the ankle-joint independently, as usual; after passing which, generally about one-third down the tarso-metatarsus, they blend completely, *before* any slip has been given off. From the conjoined tendon thus formed the tendons of distribution spring, four in number, one to the hallux, and others to each of the three anteriorly directed toes [he here directs attention to his figure of *Buceros rhinoceros* to show it], that to the former being generally separated off before any of the others." (*op. cit.* p. 294.)

Upon carefully examining these parts in my specimen of *Speotyto*, I find the arrangement a little different even from any of these; in the leg we find both the flexor muscles distinct, and their tendons remain distinct to a point about four or five millimetres *below* the hypotarsus, where they not only completely



blend, but coössify, forming by their union a strong, straight, bony rod, which is harbored in a very considerable groove down the back of the tarso-metatarsus, its distal end even extending a little beyond the free accessory metatarsal of the hallux. Here it splits up into four nonossified tendinous slips, which are distributed to the four digits in the usual manner.

The foregoing facts not only prove that the arrangement of the plantar tendons differs among the diurnal Raptores, but a still different arrangement is to be found in the American *Cathartidæ*, birds in no way especially related to the former; while *Speotyto* goes to show that at least one other peculiar arrangement of these tendons is to be met with among the *Strigidæ*. This Burrowing Owl has the power of reversing the hallux, but it is not the normal position of that toe. It may be as well to add here that in this specimen the tendon of the superficial flexor at the back of the tarso-metatarsus is also completely ossified.

#### THE VISCERA AND CERTAIN OTHER STRUCTURES.

An examination of the heart and great vessels reveals the fact that the first-mentioned organ is comparatively large for the size of the bird, and elongated rather than of an ovoid shape. Both carotids are present, and ascend the neck to the head through the usual canal intended for them on the anterior aspect of the cervical vertebræ.

Turning to the *trachea* and *syrinx*, we find the former for its lower half, somewhat compressed from side to side, the reverse of the case in the upper part of this tube. Its rings are ossified; not so, however, the ring of the bronchi. Two of the semi-rings and the *pessulus* are ossified, and the former open wide apart posteriorly. But two pairs of muscles appear to be present, the "sterno-tracheales," and the "tracheo-laterales."

The *liver* is divided into *two* very nearly equal-sized lobes, joined with each other by a very slender band; and I fail to discover the presence of any *gall-bladder*.

Of considerable calibre, the *œsophagus*, including the *proventriculus*, has a total length of 9.5 centimetres, the latter organ merging gradually into the ovoid and somewhat muscular gizzard. This is lined with a firm corneous coat, and the pouch when opened contained a few large black beetles, being in a

partly digested condition. The thickest part of the wall of the gizzard is about 4 millimetres; this is at its posterior aspect, and quite near the proventriculus. Coues has stated (*Key*, 2d ed., p. 498) that the Owls have "short and wide intestines," but not so, judging from the specimen before me, the Burrowing Owl, *Speotyto*, as in it the intestine is of unusually small calibre, and *very long*, measuring from stomach to anus no less than 39 centimetres. Each cœca has a large bulbous extremity though its pedicle is very slender; it measures 3.4 centimetres, and it springs from the intestinal tube (at the same point with its fellow), 4.6 centimetres above the anal opening.<sup>1</sup>

Other organs and parts presented in the economy of this Owl were examined quite in detail by the writer, but nothing of very great import was discovered, beyond what is common to the morphology of the group as a whole. The specimen chiefly used by me in these dissections was extraordinarily fat, especially at the root of the neck, and overlying the flanks, and lower part of the dorsum and abdomen.

This Owl, in common with some other *Striges*, has an antero-posterior foraminal perforation through either coracoid, a fact which I pointed out in my memoir in the Osteology of the bird, and I further said there, that "this foramen transmits a branch of that cervical nerve coming from between the twelfth and thirteenth cervical vertebræ."<sup>2</sup> More strictly speaking, I find upon reëxamination, that although I have given the nerve's exit correctly, in reality it is the anterior branch of the brachial plexus, and after passing through the aforesaid foramen in the shaft of the corresponding coracoid, from behind, forwards, it is distributed to the *pectoralis secundus* muscle, following its tendon on the aspect next the body of the sternum, while the minute nerve-fibres branch up among the fibres of the muscle. This same interesting condition obtains in *Bubo virginianus*, and some Hawks of the genus *Buteo*.

<sup>1</sup> Both the intestine and mesentery in this specimen of *Speotyto* had sparsely sprinkled over them, sometimes in groups of four or five, and sometimes singly, little ovoid bodies about the size of No. 10 shot, pure white in color, and having all the appearances of lime-like deposits in the tissues where found.

<sup>2</sup> SHUFELDT, R. W., *Contributions to the Anatomy of Birds*, p. 612.

## CONCLUDING REMARKS.

The notes offered in the present paper may fitly be considered as supplementary to my more extended memoir upon the *Osteology of Speotyto*, already alluded to above. I look forward with pleasure to some day devoting considerable attention to the American Raptorial Birds as a group, and from what I have thus far seen of them I have every reason to believe that they will afford characters of more than usual interest; the Owls, in particular, are, in many instances, very dissimilar in their skeletons and probably so in other systems of their economy. Anatomically, too, the Hawks, Falcons, and Eagles offer much that requires thorough investigation, and for this work, the writer is continually employed in bringing together his material.

My researches upon the anatomy of *Speotyto*, as here set forth, most conclusively go to show that our American species of Owls — and there are a number of them — require far more extended investigations of their pterylography than they have received up to the present time. *Speotyto* offers, as I have shown, peculiarities in this regard, not observed by that great investigator of this subject, Nitzsch, and what I have here described, surely needs comparison with a number of our *Strigæ*, and I dare say with forms from the avifaunæ of other countries where Owls occur.

Another matter which needs attention, is to ascertain which of our Owls possess a *vomer*, and which do not; it would seem that this bone of the cranium never ossifies in this Prairie Owl; another interesting fact.

Further comparison is needed of the patagial group of muscles in these birds; indeed, it would repay the labor to make quite an exhaustive study of this for the diurnal and nocturnal Raptores, to include the *Cathartidæ*. *Speotyto*, as I have shown, has peculiarities in this direction also.

Again, the arrangement of the *plantar tendons* sadly needs looking into, and thorough comparisons made in the groups to which I have just referred. What has been brought out in the present paper, goes to prove that our subject here also affords structures at variance with the known arrangement of the same parts in certain diurnal birds of prey.

And so on through the remainder of the economy of *Speotyto*,

much of which affords, here and there, other suggestive characters. Nevertheless it is very plain to be seen, from all this, that at the present writing it cannot be predicted with safety what are the nearest affines of this Owl as indicated by a complete knowledge of strigidine morphology ; but the writer feels that he has the right to hope that the present outline, with the salient features in the anatomy of this unique owl, presented as they here are, may assist to some extent the solving such problems.





## VARIATION OF THE SPINAL NERVES IN THE CAUDAL REGION OF THE DOMESTIC PIGEON.

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ONE of the most conspicuous of the variations in the internal structure of the common domestic pigeon, is that which affects the number of the vertebræ in the caudal region. These ordinarily vary from five to eight between the sacrum and coccyx; and it was the purpose of this work to determine whether the pairs of spinal nerves vary in the same ratio, or whether they remain constant in number and position of exit from the vertebral canal, without reference to the number of vertebræ themselves.

The methods were first by dissection, and the accuracy of the results so gained was then tested upon the same and other specimens by cutting sections. Before dissecting, the whole caudal region was taken from the bird, the muscles and connective tissues removed from one side so as to determine accurately the number of free vertebræ, but left upon the other side so as to leave all spinal nerves intact. The part was then placed for a fortnight or more in an aqueous solution of picric acid until the nerves were hardened and the vertebræ somewhat decalcified, so that their processes could be cut easily with a sharp scalpel; the specimen was then pinned out under water, the neural arches cut away, and the cord and pairs of nerves so exposed were traced out under a lens with bent needle points. A considerable number of birds were dissected in the fresh state also, but with less certainty about the last nerves. For cutting sections, a much longer decalcification in picric acid was required before the centra of the vertebræ would become sufficiently pliable, and a maceration in a ten per cent solution of nitric acid for two or more days was found to be more expeditious. Borax carmine and hæmatoxylin were used for staining, and the material imbedded in paraffine.

In most cases the dove-cote pigeon possesses six free caudal vertebræ and the coccyx; but not infrequently specimens are found with seven free vertebræ, the fan-tail with eight or seven, while sometimes cases are found with as few as five. In a paper on the gallinaceous birds,<sup>1</sup> W. K. Parker says: "I do not set so much value on the number of caudal vertebræ, as the last is a series, and the tail is very apt to vary in the number of those which shall be swallowed up in the terminal piece. The sacral are easily distinguished from the caudal in these birds, as even in the pigeons the caudal are no longer pneumatic; that is a better character even than the coalescence of a vertebra with those that precede it." Thus in the pigeons the variability extends not only to members of different orders of birds, but is marked in the same species and may be more or less fixed by selection, as in the fan-tails, which ordinarily have eight or nine caudal vertebræ, according to Darwin,<sup>2</sup> and possibly ten. The coccyx from the very nature of its composition is of varying length and curvature; these features being determined perhaps by the more or less complete fusion of a vertebra to its anterior end, while the connective tissue which attaches to it and bridges over from it to the adjoining vertebræ, forms a convenient medium of ossification tending toward the obliteration of the last and smallest vertebra in the compact mass of connective tissue for the insertion of the rectrices. But it can hardly be said that the number of free vertebræ depends upon the freedom or fusion of the last one with the coccyx, for in this case we should expect to find a long coccyx following a short series of caudal vertebræ, and a short coccyx where the most vertebræ are free from it; whereas the facts would indicate that a large number of vertebræ is followed by a longer coccyx, so that in the cases having seven or eight free vertebræ the coccyx is longer than in those possessing five or six (cf. *c* in Figs 1-4), suggesting some other cause for the lengthening of the whole region, as a result of which more vertebræ are left detached from the terminal piece; so that as the whole region is lengthened or shortened the coccyx lengthens or shortens in about the same ratio. But it is often quite difficult to determine the exact length of the coccyx, on account of its imperfect union with the preceding vertebra.

<sup>1</sup> *Transactions of the Zoölogical Society of London*, Vol. V., p. 198.

<sup>2</sup> *Animals and Plants under Domestication*, Vol. I., p. 205.

In close relation to the varying vertebræ stand the spinal nerves. The dorsal ganglion is very prominent, being smaller in size and farther from the cord in the most posterior pairs of nerves. Shortly beyond the ganglion the nerve branches, — one branch sinking below the lateral process of the vertebra and supplying the muscles beneath, the other and smaller running backward in the muscles dorsal to the vertebræ. In the ordinary dove-cote pigeon, of six free caudal vertebræ, there would be seven intervertebral spaces in which the outgoing spinal nerves would lie if they existed (Fig. 2,  $s_1-s_7$ ); but on account of the mass of connective tissue which invests the coccyx and terminal vertebræ, for the attachment of muscles and quills of the large tail-feathers, the terminal segments of the vertebral column seem to have lost their independent action and to have become more or less anchylosed; the cord within is degenerated into a large filum terminale which gives off no nerves posterior to the fifth space, Fig. 2,  $s_5$ . Thus the dissection of the common birds, represented in Fig. 2, would ordinarily reveal a series of six free caudal vertebræ and seven intervertebral spaces, and a continuous series of paired spinal nerves ( $n_1-n_5$ ), leaving the neural canal between these vertebræ as far backward as the fifth space,  $s_5$ ; leaving the last two spaces without nerves, while the cord is continued on far into the coccyx as a large filum terminale, gradually diminishing in size until it runs out. The nerve roots are seen in the dissected cord to originate some distance anterior to the point of exit. A bird having only five free caudal vertebræ is comparatively rare, and yet the same relation between nerves and vertebræ seems to exist as in the more common form with six. Thus the dissection represented in Fig. 1 shows a series of only five free vertebræ, six spaces ( $s_1-s_6$ ), and a continuous series of nerves, which stops short, however, of the last two spaces as in the former case (Fig. 2), thus showing a reduction of the cord in accordance with that of the bony investment. The filum, as before, is continued far into the coccyx. The vertebræ in this specimen were all very distinctly made out, as there was no imperfect union either with the sacrum or with the coccyx. A variation by the increase of the number of free vertebræ to seven is more commonly met with. Darwin states that this is the normal constitution of the rock pigeon;<sup>1</sup>

<sup>1</sup> *Animals and Plants under Domestication*, Vol. I., p. 205.



and in two of the fans used in this work there were only seven caudal vertebræ actually free, the eighth being imperfectly anchylosed with the end of the coccyx, and in several other ordinary birds the same number obtained. No especial reason could be given for this increase in the series, since the birds did not differ materially from the others in size, nor were any of the variations apparently more common in one sex than in the other, although two birds with seven vertebræ and one with six vertebræ were male, four with six and the one with five vertebræ were female, all having been taken at random from the belfry of a church. But the ratio of variation was much greater in this lot than is the rule, for in the thirty-odd specimens examined, there was no other case of five vertebræ found, and a smaller percentage with seven vertebræ would usually be found than occurred in this lot of six birds. So also a large white male fan with twenty-six tail-feathers was provided with only seven actually free vertebræ, the same number as an ordinary common male bird possessed. But the dissection of such a specimen with seven free vertebræ shows again that the series of nerves is coincident with the series of vertebræ between which they are given off, as far backward as to leave only the last two spaces without nerves (Fig. 3,  $s_1-s_8$ ,  $n_1-n_6$ ), adding  $n_6$  to fill  $s_6$  upon the addition of an  $s_8$  beyond  $s_7$ . The most remarkable development of the caudal region is naturally found in the fan-tail, since the efforts of selection have been directed toward this part of the body in inducing a wide expanse of tail-feathering. The usual number of eight vertebræ was found, but in two cases the eighth, or last, was imperfectly anchylosed to the coccyx, so that although the neural arch was plainly separate, yet the body of the vertebra was immovably united with the coccyx. A dissection of a specimen with eight actually free caudal vertebræ is represented in Fig. 4, where by the further addition of another vertebra the intervertebral spaces become nine ( $s_1-s_9$ ) in number; and here too another nerve,  $n_7$ , appears in  $s_7$ , augmenting the series so as to keep  $n$  constant with  $s$ ; *i.e.*, the last two spaces only in the series of vertebræ are left without nerves as in the other cases.

Thus far it will be seen from a series of dissections that the supply of nerves from the cord is constant with the series of vertebræ; a change in the latter is followed by a corresponding

change in the former. But cases are often found in dissection which show that the supply of spinal nerves is not always constant in this relation to the number of vertebræ, so that nerves may appear in the next space behind, in one of the two that are often, if not ordinarily, left vacant. Thus Fig. 5 represents such a dissection where a new term  $n_6$  is introduced into  $s_6$  of a series of six free caudal vertebræ. A comparison with Fig. 2 will show that the nerve supply has undergone less reduction by one pair of spinal nerves proceeding into  $s_6$ ; or that the nerve supply is here better developed than in other cases. The same variation was met with in dissections of specimens with seven free caudal vertebræ, so that another figure might be drawn in all respects similar to Fig. 3 with the exception that an  $n_7$  would appear in  $s_7$  (cf. Fig. 3). This was made out in a large white male fan with seven actually free vertebræ, and no less distinctly in a common dull-colored male bird of the same number. The other cases of seven vertebræ that were dissected proved to be as represented in Fig. 3. This occurrence of the extra pair of nerves is of course merely the fulfilling of ordinary conditions of the spinal column, which here may or may not take place, just as the last vertebræ in the series may or may not be articulated with the coccyx, instead of being ossified with it. And there is no reason to suppose that the very last space might not in some cases be furnished with nerves also, although there is no evidence of this occurring in the many specimens examined.

Sections of the vertebral column and the cord in place show the arrangement of the investing membranes, the relative size and structure of the filum terminale, the lumen of the cord, and the exit of the nerves. The dura mater investment extends to the extremity of the vertebral canal, which runs at least three-quarters of the length of the coccyx. This membrane contains blood-vessels running in it, one of which passes up into the pia mater, in which it may be traced far forward; it is in connection with this that the pia mater and the end of the filum first appear, some twenty sections anterior to the end of the spinal canal. The lumen of the cord itself first appears in the filum within five or six sections of the end. Thus the relations of the pia mater, the blood-vessel, and the lumen of the cord are shown in Fig. 6; — the section being much magnified, so that the space between the dura mater and the pia mater is not brought into the field.

The central lumen or canal of the cord is seen to be very prominent at this point, and is surrounded by a dense row of nuclei, which are those of the epithelium lining the canal. The exact nature of the other mass of nuclei that are collected within the investing membrane is not easy to determine. Some of them are quite large and show a distinct nucleolus, a few may be from the gray matter, and some connective tissue nuclei. A neuroglia also exists to some extent, — enough to form a kind of matrix for the nuclei. As the filum passes forward, the same general structure is seen, but its actual size is much increased, the nuclei becoming fewer, and the neuroglia consequently more distinct. Thus Fig. 7 represents a section taken beyond the coccyx on the posterior face of the last free vertebra; *i.e.*, in the anterior part of  $s_7$  in Fig. 2. The filum has increased in size, and the lumen is lined by a row of columnar nucleated cells, while in the other parts the nuclei are less thickly distributed than in the former section. The dura mater investment lines the neural arch cavity, and the pia mater closely invests the filum itself, being thicker upon the lower side. It is from this lower side of the pia mater investment that connective tissue processes are given off which go out to the dura mater and serve to support the cord in place. In this region they are not numerous, but they are seen in serial sections attached to the dura mater and to the pia mater; they are sometimes oblique, and are then to be carefully distinguished, when viewed under low powers, from nerves lying in the cavity. Blood-vessels are now abundant in the dura mater, and smaller ones in the pia mater. Passing forward into the next anterior space ( $s_6$ , Fig. 2) and selecting a section well forward so as to include the position of outgoing nerves, the structures take the form represented in Fig. 8. The connective tissue arch between the including vertebrae becomes somewhat broken through in part, and allows the exit of blood-vessels that pass to parts beneath; but in this, as in all the sections of this vertebra, — cutting anteriorly, — no pair of nerves lying near the cord is cut. The lumen of the cord — still lined by the nucleated cells — is becoming relatively smaller, the size of the filum terminale itself is increased, and together with the investing membranes takes on more of the characters of the cord proper. A section in the next intervertebral space ( $s_5$ , Fig. 2) includes the last pair of



spinal nerves ( $n_5$ , Fig. 2) as they leave the vertebral column. In a series of sections running anteriorly these nerves are at first, of course, cut diagonally at some distance from the cord itself, since they enter the neural canal obliquely; and a section at that point shows them near to the cord, lying within the neural arch (Fig. 9,  $n$ ). Passing within the neural canal, the nerve does not immediately become attached to the cord, but runs for a time quite above it in the dura mater investment; finally it comes to lie within the latter, and passes more anteriorly into the pia mater close to the cord, in which it is contained until all the fibres have passed into the cord itself,—some distance therefore anterior to the place of exit. So that while cutting through one of the more anterior vertebræ the nerves destined to pass out in the next posterior space are found lying beside the cord, yet these pass into the structure of the cord before the exit of the next anterior pair of nerves from the spinal canal; *i.e.*, only one pair of nerves lying parallel with the cord will appear in any given section. And so the “brush-like” arrangement of the nerves from a definite end of the cord, as is found in mammals, is not strictly the case here, although the point of attachment of each pair of caudal nerves to the cord is anterior to their place of exit from the vertebral column, as in the former case. No definite region could be determined as the place where the gray matter of the cord begins. It seems rather to accumulate insensibly—in sections running forward—about the central lumen of the cord until the cornua take their characteristic shape. Cells belonging to the gray matter are present doubtless in greater or less quantities throughout the filum, so that the latter seems to be merely a continuation of the cord that does not give origin to spinal nerve roots. There seem to be no definite tracts in which these ganglion cells are laid, but such are definable a little anterior to the elongated origin of the roots of the last pair of nerves. The ganglion upon the dorsal root of the more posterior pairs of caudal nerves is situated farther from the neural canal, and is also much smaller, but in the more anterior parts of the caudal region the ganglion lies in the intervertebral space, and sections pass through it at a very slight angle. Such a section taken in  $s_3$  or  $s_4$  shows the structure of the ganglion lying in the space, as in Fig. 10. Upon the right side of the figure the proximal part of the ganglion is cut



through, showing its extraordinary length and size, and the large cells interspersed with fibres. These cells are very large, sometimes measuring  $36\mu$  in length, and  $24\mu$  in breadth. On account of the obliquity of the plane of section, both the dorsal and ventral roots are shown upon the left side of the figure before their union, showing again the great length of the ganglion structure upon the dorsal root of the more anterior caudal nerves.

Owing to the difficulties of distinguishing the nerves that might occur in the last two spaces in the dissections, on account of the abundance of connective tissue that obscures them, it is possible that a great number of specimens devoted entirely to sections might show a larger proportion of cases where nerves occur in the anterior one of these spaces. But the results are the same in any case, namely, that by the lengthening of the caudal series of vertebræ, the nerve supply from the cord follows in the same, if not an increased ratio; and that the series of nerves is always continuous, *i.e.*, consecutive. As there are different degrees of anchylosis between the last vertebræ and the coccyx in different specimens of the same flock, so are there different degrees of nerve supply from the cord. And especially as the last vertebra is most variable, so is the nerve in this space preceding it. Indeed, one series of sections was made in which there seemed to be only a single nerve leaving the cord in the last space but one, its fellow being wanting on the other side; and one specimen had the same appearance in dissection. The last vertebra is often found with its neural processes as free as any of the others, but with its centrum firmly anchylosed with the coccyx of which it thus forms a part. Sections also show that the filum terminale is a structure of some importance and complexity, and runs far into the coccyx, carrying the two investing membranes, the dura mater and pia mater, the former of which extends to the extreme end of the spinal canal; and that the lumen of the cord persists very plainly to the end, where it closes; also that there is no "cauda equina" exactly comparable with that which is found in mammals, since the nerves originate from the cord at considerable intervals from each other; and finally, sections give added evidence to the ready variability of the central nervous system in correlation with other parts.

This work was suggested, and to a great extent directed, by Prof. S. F. Clarke, for whose aid in procuring material, and many laboratory facilities, and for whose kindness, I am much indebted.

BIOLOGICAL LABORATORY, WILLIAMS COLLEGE, June, 1888.

## EXPLANATION OF PLATE VIII.

The dissections are all drawn to a scale.

FIG. 1. Five caudal vertebræ. The letters  $s_1-s_6$  indicate the intervertebral spaces. The letters  $n_1-n_4$  denote the nerves as far as they occur in the spaces.  $c$ , the coccyx.

FIG. 2. Six free caudal vertebræ. Letters as before, showing the addition of another vertebra, and so of  $s_7$ , with the corresponding addition of  $n_5$ .

FIG. 3. Seven free caudal vertebræ,—with corresponding addition of  $s_8$ , followed by the occurrence of another pair of nerves,  $n_6$ .

FIG. 4. A fan-tail with eight free caudal vertebræ, increasing the intervertebral spaces by  $s_9$ ; another pair of nerves now found in space seven.

FIG. 5. Showing the ordinary number of six vertebræ, and spaces  $s_1-s_7$  (compare with Fig. 2), but the usual number of nerves is increased to  $n_6$ , which does not occur in Fig. 2. A similar variation might be indicated for Fig. 3 with its seven vertebræ.

The sections, except Fig. 6, were drawn with an Abbé camera, Zeiss objective A, and ocular 2.

FIG. 6. A section of the filum terminale taken very near its extremity in the coccyx.  $p.m.$ , the pia mater investment;  $l$ , the lumen surrounded by nuclei;  $b.v.$ , the blood-vessel. This section was drawn with objective D, ocular 4.

FIG. 7. Section taken in  $s_7$  (of Fig. 2), showing that no nerves leave the cord in this space.  $n.a.$ , neural arch of vertebra;  $f$ , filum terminale;  $p.m.$ , pia mater;  $d.m.$ , dura mater;  $a.t.$ , adipose tissue.

FIG. 8. Section taken in  $s_6$  (Fig. 2), showing the absence of outgoing nerves.  $n.a.$ , neural arch of vertebra;  $f$ , filum terminale;  $a.t.$ , adipose tissue.

FIG. 9. Section through  $s_5$  (Fig. 2), showing the presence of the last pair of outgoing pair of spinal nerves.  $n.a.$ , neural arch;  $n.$ , nerves cut obliquely;  $f$ , filum terminale.

FIG. 10. Cross-section of cord in place taken more anteriorly,—in  $s_3$  or  $s_4$ ,—including a longitudinal section of the long ganglion,  $g$ , on the dorsal root of the nerve;  $n.a.$ , the neural arch of vertebra;  $p.m.$ , pia mater;  $d.m.$ , dura mater;  $l$ , the lumen of the cord;  $g$ , the ganglion. The section, being taken a little obliquely, shows the two roots of the nerve upon the left side before their union. On the right side the ganglion cells are shown in the outgoing dorsal root.







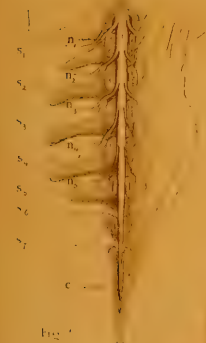
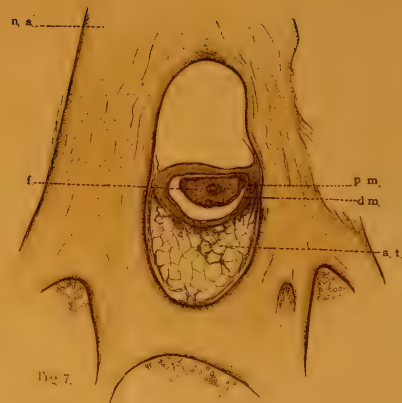
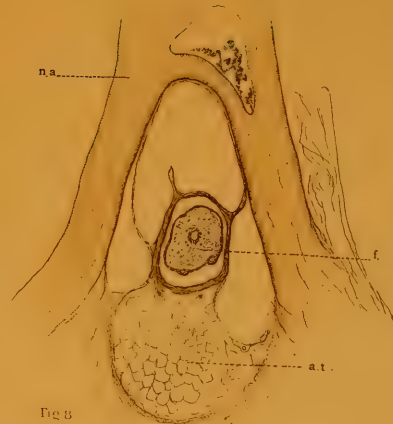
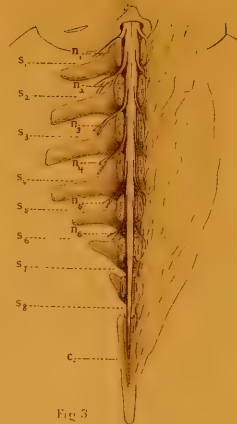
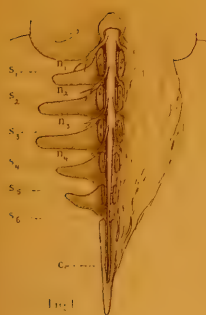


Fig. 4

Fig. 5

Fig. 3

Fig. 7

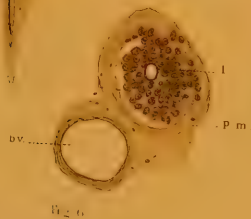


Fig. 6

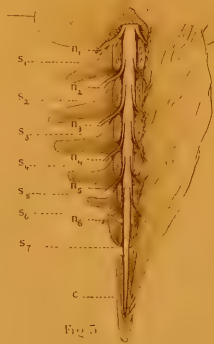


Fig. 5

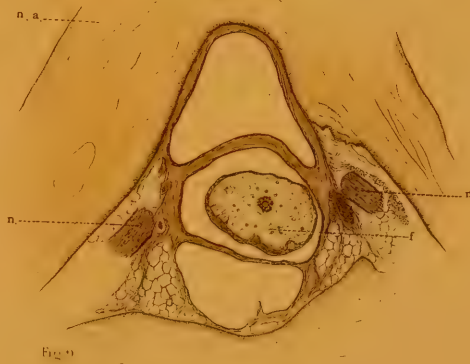


Fig. 9

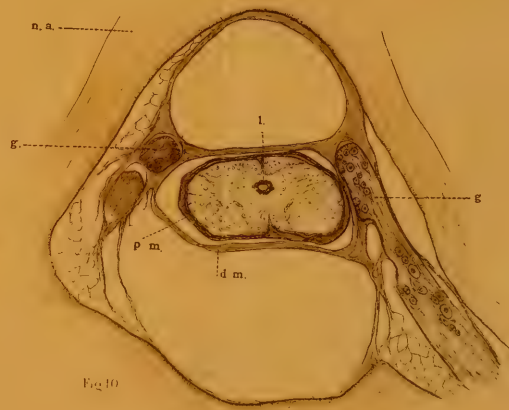


Fig. 10



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## THE MECHANICAL CAUSES OF THE DEVELOPMENT OF THE HARD PARTS OF THE MAMMALIA.

E. D. COPE.

ALTHOUGH three-quarters of a century have elapsed since Lamarck formulated the causes which produce variation in organic beings, but little has been done towards tracing the immediate action of those causes. The father of organic evolution ascribed some of these modifications of structure to changes in the environment, some to the motions of the organic being, and others to both combined.<sup>1</sup> Spencer in 1865<sup>2</sup> devoted a short chapter to the effect of motion in producing variations, and specified the mechanical effect of flexure in producing segmentation of the vertebral column. The present writer, in 1871,<sup>3</sup> insisted on the importance of motion as a factor in determining growth, and in 1872<sup>4</sup> approached the subject more definitely in the following language: "The first physical law is that growth force . . . must develop extent in the direction of least resistance, and density on the side of greatest resistance." In 1877 Ryder further applied the principle of motion to the origin of structural changes in the feet of Mammalia, in the following language:<sup>5</sup>

<sup>1</sup> *Philosophie Zoologique*, Chap. VII., 1809; translation in *American Naturalist* for 1888.

<sup>2</sup> *Principles of Biology*, II., pp. 167 and 195.

<sup>3</sup> *Proceedings of the American Philosophical Society*, p. 259; Origin of the Fittest, 1887, p. 210.

<sup>4</sup> *Penn Monthly Magazine*; Origin of the Fittest, 1887, p. 30.

<sup>5</sup> *American Naturalist*, 1877, p. 607.



"1. That the mechanical force used in locomotion during the struggle for existence has determined the digits which are now performing the pedal function in such groups as have undergone digital reduction. 2. That where the distribution of mechanical strains has been alike upon all the digits of the manus or pes, or both, they have remained in a state of approximate uniformity of development." In the same year, in discussing the origin of the great development of the incisor teeth in the Rodentia,<sup>1</sup> Professor Ryder, in summing up, ventured "the reflection that the more severe strains to which they were subjected by enforced or intelligently assumed changes of habit, were the initiatory agents in causing them to assume their present forms, such forms as were best adapted to resist the greatest strains without breaking." In 1878 the writer<sup>2</sup> advanced the following proposition: "Change of structure is seen to take place in accordance with the mechanical effect of three kinds of motion, viz., by *friction, pressure, and strain.*" In the same year Professor Ryder went into a discussion of the specific application of strains in the evolution of the dental types of the Diplarthrous Ungulata, and prepared the field for work in the Rodentia and Proboscidea.<sup>3</sup> In 1879 the writer gave mechanical reasons for the reduction of the sectorial teeth of Carnivora to one, and for its present position in the jaws.<sup>4</sup> In 1881 the writer<sup>5</sup> described the specific action of impacts and strains in the production of the existing characters of the articulations of the limbs in the higher Mammalia. In 1887 the same subject, together with that of the mechanical origin of the characters of the molar teeth, was more fully investigated in a paper on the Perissodactyla.<sup>6</sup> In 1888 the writer published a paper on the mechanical origin of the sectorial teeth of the Carnivora,<sup>7</sup> one on the mechanical origin of the peculiar dentition of the Rodentia,<sup>8</sup> and a third on the mechanical origin of the dentition of the Amblypoda.<sup>9</sup> In 1889

<sup>1</sup> *Proceedings Philadelphia Academy*, 1877, p. 318.

<sup>2</sup> *American Naturalist*, 1878, January; Origin of the Fittest, p. 354.

<sup>3</sup> *Proceedings Philadelphia Academy*, 1878, p. 45.

<sup>4</sup> *American Naturalist*, March, 1879.

<sup>5</sup> *American Naturalist*, April and June, 1881.

<sup>6</sup> *American Naturalist*, 1887, pp. 985, 1060.

<sup>7</sup> Read before the American Association for the Advancement of Science, New York, 1887, p. 254.

<sup>8</sup> *American Naturalist*, January, p. 3.

<sup>9</sup> *Proceedings of the American Philosophical Society*, 1888, p. 80.

the writer discussed the mechanical causes of the structures of the elbow and other joints, in the Artiodactyla, and the origin of the peculiar intervertebral articulations in that order.<sup>1</sup> This enumeration covers, so far as I am aware, the work done in this field. A good deal of it has been tentative, while to other portions of it considerable precision and conclusiveness may be granted.

At the present time we are in a position to understand what the structural changes are, which the Mammalia have gradually acquired through the operation of causes long continued through geologic time. In other words, we are now, thanks to vertebrate paleontology, in possession of the phylogeny of most of the lines of Mammalian descent. We are thus able to distinguish between primitive characters and characters of degeneracy. We can understand the origin and progress, and also the decadence, of structural characters. The more my attention has been directed to the facts thus presented, the more convinced I have become that, in the language of Lamarck, it is the habit that has given rise to the structures of animals, and not the structures which have forced animals to adopt their special habits.

In the following pages the salient characters of the skeleton and of the dentition of the Mammalia are examined, and the attempt is made to discover in the light of the descent traced by paleontology, the mechanical causes for their existence. It is believed that in a considerable proportion of instances this attempt has been successful; while in others a tentative stage only has been reached. The intelligent reader will be able to determine to which category any given discussion may be referred.

The position of the Post-Darwinians is clearly set forth in an abstract of a lecture delivered by Prof. E. Ray Lankester, at the London Institution, which appears in *Nature* of February 28, 1889. Professor Lankester declares that the error of Lamarck (and consequently of the Neolamarckians) consists in the assumption that acquired characters can be inherited. He says: "Congenital variation is an admitted and demonstrable fact; transmission of congenital variations is also an admitted and

<sup>1</sup> *American Naturalist*, March, 1889.

demonstrable fact. Change of structure acquired during life — as stated by Lamarck — is also a fact, though very limited. But the transmission of these latter changes to offspring is not proved experimentally; all experiment tends to prove that they cannot be transmitted." Two inferences may be derived from these statements. First, the author of them does not believe that the so-called congenital variations can be or have been acquired; second, that he has no hypothesis to offer in explanation of the origin of congenital variations. These positions exclude another inference, which nevertheless may be derived from other propositions embraced in the abstract of the lecture. He says, with Lamarck, that "change of structure acquired during life is also a fact," and also that "all plants and animals produce offspring which resemble their parents on the whole." But in spite of these statements we are to believe that if a plant or animal acquires a useful addition to or modification of its structure during life, this is the particular variation which will *not* be transmitted. Since the modifications acquired by use during life are necessarily useful, it seems that according to the Post-Darwinians, the only way of acquiring useful variations known to us, is excluded from the process of organic evolution. To say the least of it, probabilities are severely taxed by such a position as this.

But we say further, with Professor Cunningham, that were this hypothesis true, there would have been no evolution. If acquisition during lifetime is to render a character non-transmissible, the continued growth of a single character by accretions during successive generations through geological ages could not and ought not to occur. Each generation should begin where its ancestors began in the matter of useful characters, or those acquired by use, so that there could be no accumulation or development of such characters. The influence of the environment, as well as that of the energies of the living being, would be incompetent to develop more in a given generation than that generation could acquire in its single lifetime. How then can evolution account for the law so beautifully displayed by paleontology, of the gradual modification of parts through long geologic ages, towards given ideals of mechanical perfection? How can we account for the gradual perfecting of the articulations of the internal and external skeletons of those

which possess them? Not only is no explanation offered by the Post-Darwinian school, but such progress is, under their hypothesis, impossible. It is an explanation of *obscurus per obscurius*. But we are still of the opinion, in spite of Weissman's theory to the contrary, that so long as the germ plasma is subject to nutrition, it is subject to influences occurring during the adult life of an animal, and it would be an exception to all the other tissues were it not so.<sup>1</sup>

The ground covered by the present essay is only that which paleontological discovery has brought fairly within reach. The history of some parts of the skeleton in various types is yet unknown, especially as regards their function in extinct forms. The solution of these problems must be left for future research.

It has been found that in all instances where it has been practicable to observe living animals, explanations of puzzling structures were found in some peculiar habitual movement which they exhibit. In this investigation I have been, therefore, greatly aided by the Zoölogical Garden of Philadelphia and its able superintendent, Mr. Arthur E. Brown. I have also derived considerable assistance from the extensive series of photographs of animals in motion, by Muybridge, issued under the auspices of the University of Pennsylvania; and the analysis of these motions in the accompanying text by the distinguished anatomist, Dr. Harrison Allen.

It must be mentioned at the outset that bone-tissue is plastic, especially in the living state, and in time moulds itself upon resisting surfaces. The more spongy tissues modify their form in accordance with denser, when in contact. As Professor Ryder has remarked, even a substance as rigid as the enamel of the teeth yields its form to continued pressure and strain, as not less rigid rocks and stones are known to do. But in a living tissue like bone, the effect of such application of energy is evidently much greater than in any equally rigid non-living body. The metabolism of nutrition is clearly a most important factor in the production of the results, rendering the transfer and location of building material possible, which unassisted impacts and strains could not accomplish.

<sup>1</sup> *American Naturalist*, March, 1889.



# INTRODUCTORY REMARKS ON THE PHYLOGENY OF THE MAMMALIA.

The following scheme expresses the classification of the Mammalia as adopted by the writer. While it expresses the natural groupings and affinities, it is defective in that some of the definitions are not without exceptions:

- I. An interclavicle; a large coracoid bone articulating with the sternum (Prototheria Gill).  
Marsupial bones; fibula articulating with proximal end of astragalus . . . . . 1. *Monotremata*.
- II. No interclavicle; coracoid a small process coössified with the scapula (Eutheria Gill).
  - a. Marsupial bones (generally); palate with perforations; (vagina double; placenta and corpus callosum rudimental or wanting; cerebral hemispheres small). (Didelphia de Bl.)  
But one deciduous molar tooth . . . . . 2. *Marsupialia*.
  - aa. No marsupial bones; palate generally entire; (one vagina; placenta and corpus callosum well developed). (Monodelphia de Bl.)
  - β. Anterior limb reduced to more or less flexible paddles; posterior limbs wanting (Mutilata).  
No elbow joint; carpals discoid, and with the digits separated by cartilage; lower jaw without ascending ramus . . . . . 3. *Cetacea*.
  - An elbow joint; carpals and phalanges with normal articulations; lower jaw with ascending ramus . . . . . 4. *Sirenia*.
  - ββ. Anterior limbs with flexible joints and distinct digits; ungual phalanges not compressed and acute at apex<sup>1</sup> (Ungulata<sup>2</sup>).
  - γ. Tarsal bones in linear series;<sup>3</sup> carpals generally in linear series.  
Limbs ambulatory; teeth with enamel . . . . . 5. *Taxeopoda*.
  - γγ. Tarsal series alternating; carpal series linear, or reversed diplarthrous.  
Cuboid bone partly supporting navicular, not in contact with astragalus . . . . . 6. *Proboscidea*.
  - γγγ. Both tarsal and carpal series more or less alternating; the inferior row inwards.  
Os magnum not supporting scaphoides; cuboid supporting astragalus; superior molars tritubercular . . . . . 7. *Amblypoda*.
  - Os magnum supporting scaphoides; superior molars quadrutubercular<sup>4</sup> . . . . . 8. *Diplarthra*.<sup>5</sup>

<sup>1</sup> Except the Hapalidæ.

<sup>2</sup> Lamarck, *Zoologie Philosophique*, 1809.

<sup>3</sup> Except in Dendrohyrax.

<sup>4</sup> Except Pantolestes.

<sup>5</sup> This order includes the suborders Perissodactyla and Artiodactyla. It is the Ungulata of some authors.

- βββ. Anterior limbs with flexible joints. Ungual phalanges compressed and pointed<sup>1</sup> (Unguiculata).
- δ. Tarsal and carpal bones generally in linear series.
- ε. Teeth without enamel; no incisors.
- Limbs not volent; hemispheres small, smooth; mastication orthal . . . . . 9. *Edentata*.
- εε. Teeth with enamel; incisors present.
- No postglenoid process; mandibular condyle round; limbs not volent; hemispheres small, smooth; mastication proal . . . . . 10. *Rodentia*.
- Limbs volent; hemispheres small, smooth . . . . . 11. *Chiroptera*.
- A postglenoid process; mandibular condyle transverse; limbs not volent; no scapholunar bone<sup>2</sup>; hemispheres small, smooth; mastication orthal . . . . . 12. *Bunotheria*.
- A postglenoid process; limbs not volent; with a scapholunar bone; hemispheres larger, convoluted; mastication orthal . . . . . 13. *Carnivora*.
- δδ. Tarsal and carpal bones alternating.
- Fore limbs prehensile; mandibular condyle transverse; teeth with enamel . . . . . 14. *Ancylopoda*.

Paleontology has cleared up the phylogeny of most of these orders, but some of them remain as yet unexplained. This is the case with the Cetacea, the Sirenia, and the Edentata. The Marsupialia can be supposed with much probability to have come off from the Monotremata, but there is as yet no paleontological evidence to sustain the hypothesis. No progress has been made in unravelling the phylogeny of the Cetacea and Sirenia. The results attained by the study of the paleontology of the other orders may be summarized as follows:—

*First.* It is probable that the common ancestors of the placental and implacental lines of Mammalia are known to us in some of the types of the Jurassic period. Whether they were marsupial in the sense of possessing an external pouch for the young or not, is immaterial. They were probably marsupial in brain characters, in the structure of their reproductive system, and in the absence of placenta. To this source the existing polyprotodont marsupials may be traced, through such forms as *Myrmecobius*. The Multituberculate type has a cotemporary history, and one distinct from that of the Polyprotodontia, and its ancestry has not been yet discovered. Their earliest forms

<sup>1</sup> Except *Mesonyx* and some *Rodentia* and *Edentata*.

<sup>2</sup> Except *Erinaceus*.

(of the Jurassic and Triassic) are already highly specialized. They probably represent the Monotremata of their time.

*Second.* The immediate didelphian ancestors of the monodelphous Mammalia have not yet been certainly discovered. In the oldest of the latter (of the Puerco epoch) numerous points of approach to the insectivorous Jurassic forms occur, especially in consequence of the prevalent trituberculy of the molars in both epochs.

*Third.* The phylogeny of the clawed group has been traced back to a common ordinal form which has been called the Bunotheria. We trace the Carnivora back to the creodont sub-order of the Bunotheria; the Rodentia to the Tillodont; the Edentata possibly to the Tæniodont, and the Insectivora are themselves coextensive with the history of the placental series. The Ancylopoda only have undergone the alternation of the carpal and tarsal bones, which obtains in the Diplarthrous Ungulata.

*Fourth.* The phylogeny of the hoofed groups carries us back to the order Condylarthra, the hoofed cotemporary of the Bunotheria. The even and odd toed hoofed mammals are traceable back to the Amblypoda, whose oldest representatives are the Pantodonta of the Puerco. The Proboscidea and Hyracoidea come directly from the Condylarthra. Moreover, the phalanges of the lemurs are not distinguishable by any important characters from the hoofs of the Hyracoidea and Condylarthra. Not only this, but the structure of the foot in these three groups is identical in regard to the mode of articulation of the first and second rows of the tarsal and carpal bones.

*Fifth.* The characters of the feet of the Condylarthra agree with those of unguiculate placental Mammalia, and bind the two series together; a very slight modification only being necessary in the case of the foot of the Pantodonta. The synthesis of the Ungulate and Unguiculate lines is accomplished by exceptions to the characters which define them. Thus the hoofs of Pantolambda (Amblypoda), Periptychus (Condylarthra), and Mesonyx (Creodonta) do not differ by any marked character. Claws occur in the Hapalidæ of the quadrumanous line, and the ungues of some Rodentia and Edentata (Glyptodon) are absolutely intermediate between the hoofs and claws. The Bunotheria with tritubercular molar teeth are then traceable

to Condylarthra with tritubercular teeth, of which many are known from the Puerco beds, or *vice versa*; and the quadritubercular forms from corresponding quadritubercular Condylarthra, of which many are known, or *vice versa*.

*Sixth.* The anthropoid line may be traced directly through the lemurs to the Condylarthra. The changes which have taken place in the skeleton are slight, and consist among other points in a rotation of the first row of carpal bones outwards on the second row, in the anthropoid apes and man, similar to that which has occurred among the Ungulata, but it has not become so pronounced.

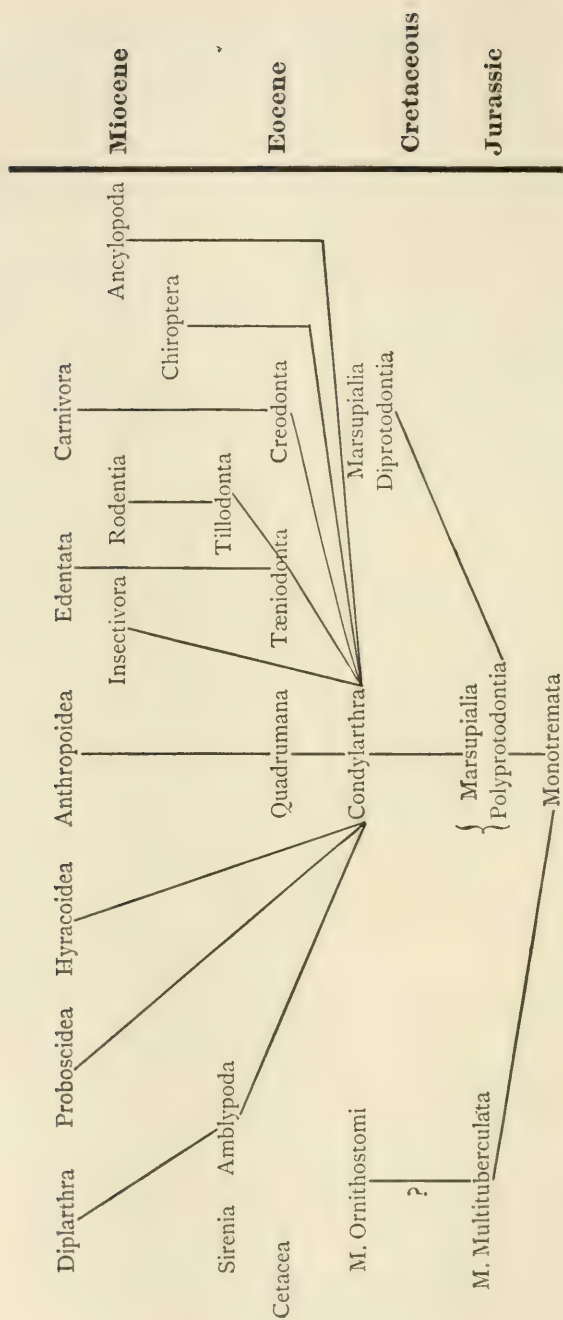
As a result we get the general phylogenetic scheme as shown on the following page.

In this diagram, divisions of greater and lesser rank are mixed, so as to display better some of the relationships. Thus all the divisions whose names stand on the right side of the middle vertical line are unguiculates; and those on the left side of the line, excepting Sirenia and Cetacea, are ungulates. The three names in the middle vertical line are those of the sub-orders of the Taxeopoda.

In the table<sup>1</sup> (p. 147), the history of some of the diagnostic characters of the Mammalia is shown, in connection with the passage of geologic time. With further knowledge it will be possible to construct similar tables explanatory of the history of the evolution of all characters of animals, so that the one now given is only preliminary.

<sup>1</sup> From the *Proceedings of the American Association for the Advancement of Science*, for 1883.





FORMATION.	NO. TOES.	FEET.	ASTRA- GALUS.	CARPUS AND TARSUS.	RADIUS.	SUPERIOR MOLARS.	ZYGAPOPHYSES.	BRAIN.
Miocene . .	1-1	Digitigrade.	Grooved.	Interlocking.	Faceted.	4-tubercles, crested	Doubly involute.	Hemispheres larger,
Upper . . . .	2-2	(Plantigrade.)	(Flat.)	(Opposite.)		and cemented.	Singly involute.	convoluted.
(Loup Fork.)	3-3							
	4-4							
Middle . . . .	(5-5)							
(John Day.)	2-2	Digitigrade.	Grooved.	Interlocking.	Faceted.	4-tubercles, and	Singly involute.	Hemispheres larger,
	3-3				Smooth.	crested.	Doubly involute.	convoluted.
	4-4							
Lower . . . .	3-3	Digitigrade.	Grooved.	Interlocking.	Smooth.	4-tubercles, and	? Singly involute.	Hemispheres small;
(White River.)	4-3	Plantigrade.			Faceted.	crested.		and larger.
	4-4							
Eocene . .	3-3	(Digitigrade.)	Grooved.	Opposite.	Smooth.	4-tubercles.	Singly involute.	Hemispheres small.
Middle . . . .	4-3	Plantigrade.	(Flat.)	Interlocking.		3-tubercles, and	Plane.	
(Bridger.)	4-5					crested.		
	5-5							
Lower . . . .	4-3	Plantigrade.	Flat.	Opposite.	Smooth.	4-tubercles.	Plane.	Hemispheres small;
(Wasatch.)	4-5	(Digitigrade.)	(Grooved.)	Interlocking.		3-tubercles, a few	Singly involute.	mesencephalon
Cretaceous .	5-5					crested.		sometimes exposed.
Upper . . . .	5-5	Plantigrade.	Flat.	Opposite.	Smooth.	3-tubercles, none	Plane.	Mesencephalon ex-
(Puerco.)						(4-tubercles, none		posed; hemisphere
						crested.)		small and smoother.
Jurassic . .						triconodont.		

## I. THE LIMBS.

The origin of the structures of the limbs of Mammalia will be considered under four heads. *First.* The proportions of the parts of the limbs. These, as is well known, vary exceedingly. The diversity is readily perceived on comparison of the four limbs of man, the horse, the whale, and the bat (Figs. 1-5-11-24); and nowhere is the relation of structure to a function of motion more obvious.

*Second.* The number of the digits. The Condylarthra have five digits on both feet, and they are plantigrade. This character is retained in their descendants of the lines of Anthropoidea, Quadrumana, and Hyracoidea, also in the Bunotheria, Edentata, and most of the Rodentia. In the Amblypoda and Proboscidea the palm and heel are a little raised. In the Carnivora and Diplarthra the heel is raised, often very high, above the ground, and the number of toes is diminished, as is well known, to two in the Artiodactyla and one in the Perissodactyla.

*Third.* The fixed articulations. In the Condylarthra the bones of the two series in the carpus and tarsus are opposite each other, so as to form continuous and separate longitudinal series of bones. This continues to be the case in the Hyracoidea and many of the Quadrumana, but in the anthropoid apes and man, the first row is partly displaced outwards so as to alternate with the second row, thus interrupting the series in the longitudinal direction, and forming a stronger structure than that of the Condylarthra. In the Bunotherian, rodent, and edentate series, the tarsus continues to be without alternation, as in the Condylarthra, and it is generally identical in the Carnivora. In the hoofed series proper, it undergoes change. In the Proboscidea the carpus continues linear, while the tarsus alternates. In the Amblypoda the tarsus alternates in another fashion, and the carpal bones are on the inner side linear, and on the outer side alternating. The complete interlocking by universal alteration of the two carpal series is only found in the Diplarthra. In the highest forms of the Rodentia and Diplarthra, the fibula and ulna become more or less coössified with the tibia and radius, and their middle portions become attenuated or disappear.

*Fourth.* The ginglymoid articulations. These include the

articulations which are flexed, extended, and rotated. Such are especially subject to the laws of motion, and it is in them that the effects of the latter are distinctly seen. As an example, the ankle joint is in the primitive Condylarthra, a flat joint, or not tongued or grooved. In most of the Carnivora, in a few Rodentia, and in all Diplarthra, it is deeply tongued and grooved, forming a more perfect and stronger joint than in the other orders, where the surfaces of the tibia and astragalus are flat, as in the Condylarthra.

#### I. THE PROPORTIONS OF THE LIMBS AND OF THEIR SEGMENTS.

The length of the legs of terrestrial Mammalia has increased with the passage of time. The inferior types of Mammalia now existing, as Marsupialia, Rodentia, Insectivora, Edentata, have short legs, with a few cases of extreme specialization as exceptions, such as Kangaroos, Rabbits, and Jerboas (hind legs only), the *Dolichotis patachonica*, the Rhynchocyonidæ and the Sloths. In the orders which stand at the summit of the series, as the Diplarthra, Proboscidea, Carnivora, and Anthropomorpha, the legs are much increased in length, and this is especially marked in certain forms which stand in all respects at the summit of their respective orders. Thus in Diplarthra, the deer, antelope, and horse are distinguished for length of limb; in the Proboscidea, the elephant; in the Carnivora, the large cats and hyænas; in the Anthropomorpha, the fore limbs are long in all, the hind ones especially so in man.

The cause of this elongation is apparently use. It is the hind legs that are elongated in a straight line in animals that walk on them, as man; and both, in those that walk on both, as the elephant. In animals that leap with the hind legs these are still more elongated, and are folded when at rest, and rapidly extended when in motion. In animals that climb with the fore legs, these are elongated, as in the Anthropomorpha except man. In those that climb with all fours, all are elongate, as in the sloths. It must be remembered that these elongations are the sum of increments added one to the other through long ages of use in geologic time. The mechanical character of that use has not been identical. It is of two principal kinds, viz.:



impact and longitudinal strain. These two forms of energy move in directions opposite to each other; the one as compression in the direction of the length of the bone; the other, as a stretching in the direction of the length of the bone. Both processes alike appear to have stimulated growth in the direction of the length of the bone.

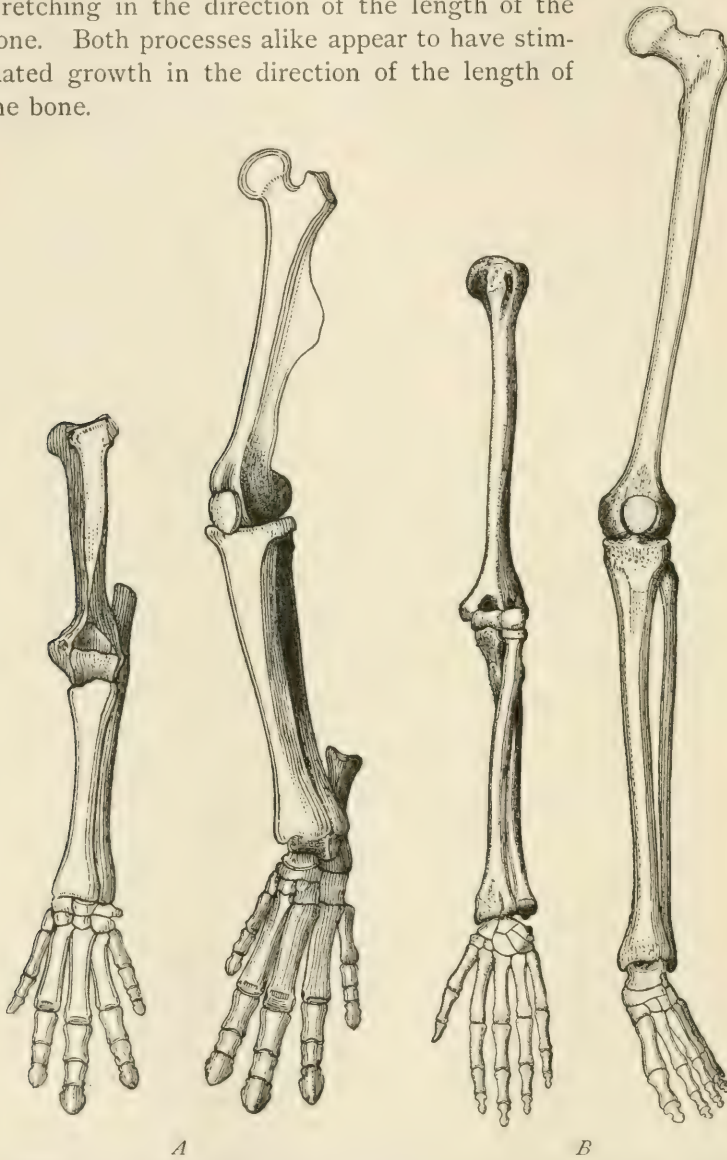


Figure 1.—A. *Phenacodus primævus*, fore and hind limbs; B. *Homo sapiens*, fore and hind limbs.

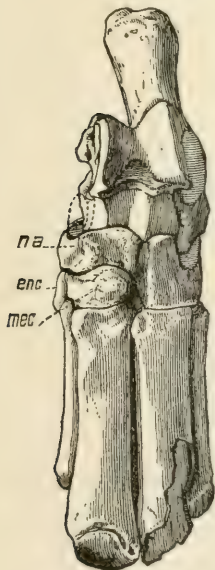
*a. Increase of Length by Impact.*

The increase in the length of the legs has not been always due to increase in length of the same segment. In a majority of the higher mammals, the increase has been principally in the foot, and especially in the metapodials and digits, producing digitigradism. In the forms which have remained plantigrade, the femur (Proboscidea), or femur and tibia (Quadrumana), or all three segments (Tarsius), have been the seat of the elongation. We can again trace these especial elongations to special uses. In animals which leap, the distal segments of the limbs are elongated; in those which do not leap, but which merely run or walk, it is the proximal segments of the limbs which are elongated.

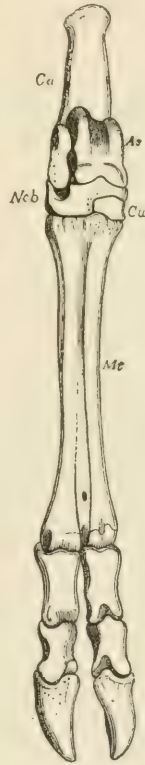
Animals which run by leaping are divided into those which run and leap with all fours, as *Diplarthra*; and those which run and leap with the posterior limbs only, as the jerboas and kangaroos. In both types, the distal segments of the hind limb are elongated, and in the *Diplarthra*, those of the fore limb also.

Animals which do not leap in progression (elephants, *Quadrumana*, bears) are always plantigrade, and have very short feet, but elongate thighs, and mostly, tibias.

These facts render it highly probable that those elements which receive the principal impact in progression are those which increase in length. In dig-



A



B

Figure 2.—Pes of (A) *Merychochirus montanus*; (B) *Bos taurus*, much reduced. *Ca.* Calcaneum; *As.* Astragalus; *Na.* Navicular; *Ncb.* Naviculocuboid; *Cu.* *Mec.*, Ecto-mesocuneiform; *Mt.* Metatarsals (cannon bone); *Enc.* Entocuneiform.

itigrade animals it is the feet which receive the impact of the repeated blows on the earth while in progression, while supporting the weight of the body at every stage of the process. In plantigrade animals it is the soles of the feet and the bones of the leg in line with them, which receive the impact, while the feet beyond this point receive none, and do not support the body except very partially at the moment of leaving the

earth. In the case of some of the *Quadrumana*, the prehensile use of the feet renders any considerable impact impossible, so the feet and hind leg generally have remained short. But in the case of the *Tarsius*, the habit of leaping has been added to the functions of arboreal progression, and the result has been a remarkable elongation of the posterior foot. But it has not been the metapodials and digits which have experienced this elongation, since they have been always employed in prehension.

It has been the tarsus proper,

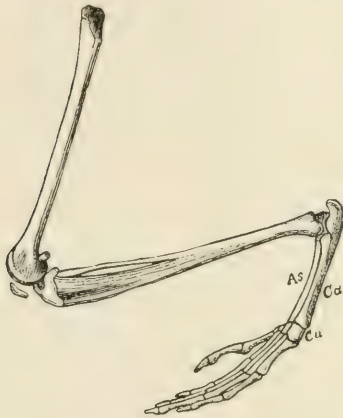


Figure 3. — *Tarsius spectrum*, posterior extremity, external side: from De Blainville.

the astragalus, and calcaneum, whose distal extremity is the very point which in a plantigrade animal must receive the impact of a leap under such circumstances.

In all of the above cases the impact is more or less directly longitudinal, or in the direction of the length of the bone, at some stage of the act of progression.

### *β. Increase of Length by Stretching.*

Examples of this kind of stimulus to the elongation of bones of the limbs are to be seen in those animals which are, for a greater or less part of the time, suspended from the limbs of trees. Such stretching must be, it is evident, in excess of muscular resistance in the opposite direction, or an opposite effect results. Thus the sloth hangs suspended from the limbs of trees, exerting apparently no muscular effort in the act, maintaining

his hold by a curvature of the claws, which was in his ancestors voluntary, but which has now become fixed by modifications of the articulations themselves. This habit has resulted in a progressive lengthening of the bones of both the leg and the foot, but especially of the leg, and most of the fore leg, which has prehensile uses not experienced by the hind leg, in serving the feeble intelligence of the animal.

A similar case of elongation through suspension is that of the fore leg of the *Quadrumana*. This modification of structure is directly as the habit of swinging by the fore leg, as in the *Ateles* of South America, and in the *Simiidæ* of the Old World. In the genus *Hylobates* the habit of progressing rapidly through the forest by swinging from the fore legs, reaches a maximum. The abandonment of this habit by man has resulted in the progressive shortening of the fore limb, both in comparison with the apes, and between the higher and lower races.

In certain types the proportions of the tarsus have undergone modifications from the same cause. In the sloths, the astragalus

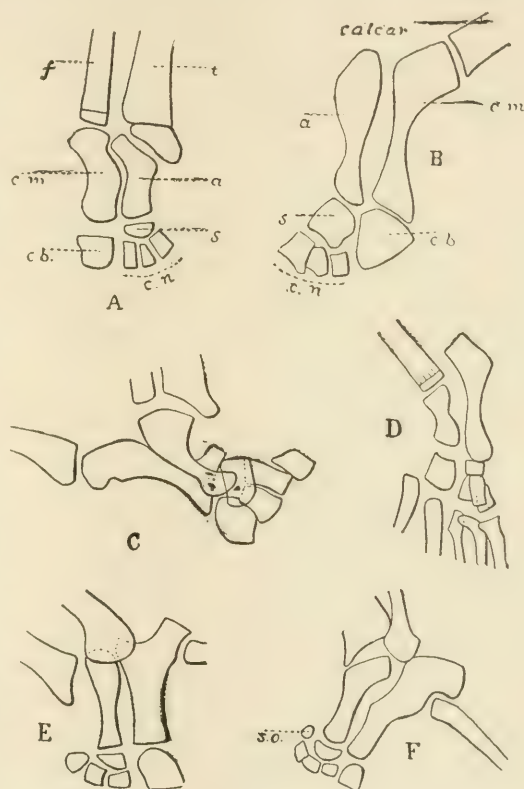


Figure 4.—Tarsi of bats, much enlarged; from H. Allen. A. *Rhinolophus capensis*. B. *Carollia brevicauda*. C. *Chilonycteris* sp. D. *Rhynchomycteris* sp. E. *Vespertilio subulatus*. F. *Atalapha noveboracensis*. Lettering: *t*, tibia; *f*, fibula; *a*, astragalus; *ca*, calcaneum; *cu*, cuboid; *n*, navicular; *1, 2, 3*, tarsalia.



and calcaneum are elongate. In the bats they are still more so, and do not possess any distinct trochlea. The greater modification of the tarsus in the bats is due to the fact that the order Chiroptera dates from the lower Eocene epoch, while the arboreal sloths originated in the Pliocene; also, perhaps, because they are suspended from the hind legs only, while the sloths hang from all four. In the latter the carpus does not share considerably in the elongation of the tarsus, but the phalanges are greatly elongate. In the Chiroptera the heel of the calcaneum is the line of attachment of a dermal membrane through which it has experienced a continual lateral strain. Concomitantly, it has grown to an enormous length. It is not so easy to understand the mechanical law which explains the growth of a part through lateral strain as through longitudinal strain. It is, however, not difficult to understand why this very elongate heel should become segmented off from the body of the calcaneum by the lateral strain of the caudal membrane, as it has.

*γ. Modifications through Other Use and Disuse.*

That the loss of articular condyles follows from a disuse of the articulation may be readily shown. That a segment of a limb may be shortened by a transfer of its function to some other segment may be also demonstrated. That muscular insertions have been enlarged or diminished directly as the use of the muscles inserted in them, is apparent from the facts.

The enormously developed muscular insertions of the humerus in mammals which dig are well known. Illustrations of this are seen in the existing monotremes, *Platypus* and *Tachyglossus*, the armadillos, and still more strikingly in the moles. Large development of unequal phalanges is characteristic of all these animals, but it reaches excessive proportions in the Cape anteater *Orycteropus*, and in the giant armadillo. Huge development of the muscular insertions of the humerus and of the scapula are especially noticeable in animals which pull the vegetation on which they feed to them from elevated positions or from below the earth, as in the extinct edentates of the family *Megatheriidæ*. As the sloths grew smaller in dimensions, the trees refused to yield to the diminished prehensile power of

the fore legs. The result has been that the sloths ascended the trees, and their limbs assumed more and more the character of mere suspensors of the weight of the body. Thus the muscular insertions of the humerus diminished, and their humeri are to-day furnished with weak ones only, the greater and lesser tuberosities of the head having nearly disappeared, so that the head of the humerus resembles that of other arboreal mammals, as the *Quadrumana* and *Simiidæ*.

The limbs have undergone great modifications of form in their gradual adaptation to aquatic habits. The stages of this process are to be observed first in the sea-otter (*Enhydra*), then in the seals, then in the sirenians, and lastly in the Cetacea. This succession is not given here as a phylogeny, for paleontology does not warrant any such history.

The use of a limb as an oar for propulsion in the water requires that it shall be, so far as the blade is concerned, inflexible. Such a structure has existed in all thoroughly aquatic vertebrata. This implies the immobility of the articulations, which is due to the loss of their condylar surfaces. This may be traced to disuse of such articulations. This disuse would be at first voluntary, the limb being held stiffly while used as an oar in the act of swimming. Loss of power of extension

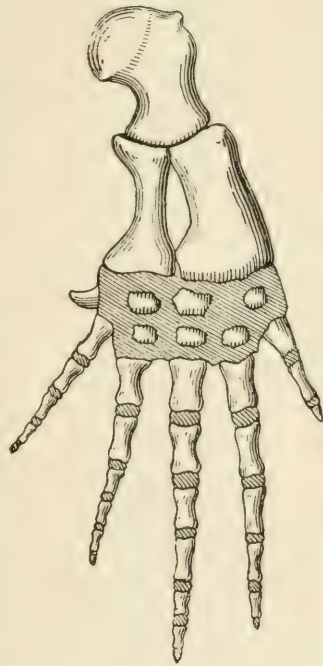


Figure 5. — *Balæna mysticetus*, fore limb: from Cuvier, *Oss. Fossiles*.

and flexion is well known to result from disuse. It is well known that the flexors and extensors of the manus have become atrophied in the Cetacea. Not so, however, with the flexors and extensors of the humerus, which become those of the entire limb. In the whales the first segment of the fore limb is enclosed within the integument of the body, so that its motion being much restricted, the insertional crests are reduced in size.

In the eared seals (Otariidæ) the hind limbs are somewhat free from the body integument, so that they can be turned forward when on land. They are further enclosed in the true seals (Phocidæ) so that their motion is very slight and they cannot be used for progression on land, and are available only for swimming.<sup>1</sup> It is supposed by Gray and Ryder that the solar and digital parts of the posterior limbs of the seals are represented in the flukes of the Cetacea. These

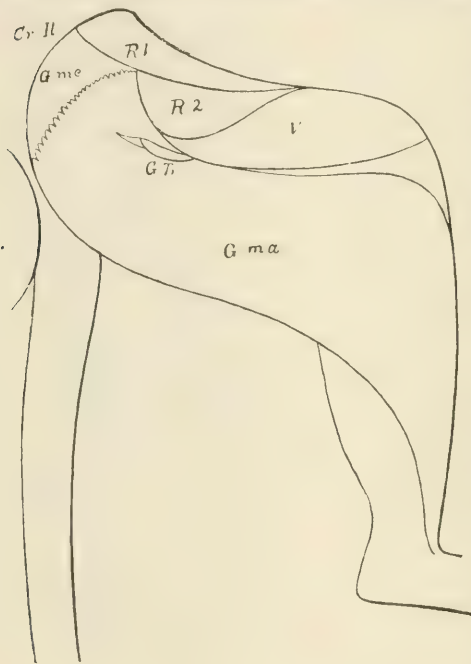


Figure 6.—Muscles of the posterior leg of *Putorius vison*, showing the position of the gluteus maximus (*Gma.*) muscle; *Gme*, gluteus medius; *R*, rectus; *V*, vastus.

parts are supposed to have separated from the proximal parts of the limbs, which have been reduced in size, and finally nearly atrophied through disuse. This view is supported by Ryder by considerations derived from studies in the embryology and anatomy of the Cetacea,<sup>2</sup> with much force. The phylogeny, however, remains uncertain, owing to our extremely defective knowledge of the extinct ancestors of their order.

The earliest approximation to the relations of the muscles and bones of the hind legs of the seals is seen in the aquatic Mustelidæ, as the otters and the mink.

In the latter (*Putorius vison*) the gluteus maximus muscle has extended its insertion all the way to the distal extremity of the tibia, thus flexing that segment, and gaining power in the stroke

<sup>1</sup> *On the Development of the Cetacea; Report of Commissioner of Fisheries of U. S.*, 1885 (1887), p. 445.

<sup>2</sup> *On the Eared Seals, Otariidæ, with Detailed Descriptions of the North Pacific Species.* By J. A. Allen. *Bull. Mus. Compar. Zoölogy*, Cambridge, II., No. 1.

of the foot against the water. This is followed by the successive shortening of the femur, which from being a lever has become a fulcrum for the tibia and hind foot. In this position, where it is comparatively fixed, it undergoes successive abbreviation and thickening, until it assumes the form characteristic of the seals (Figs. 6, 7).

Use and disuse play an important part in the determination of the forms and proportions of the phalanges. In oar-like limbs adapted to swimming, like the other segments, they lose their condyles and become immovable on each other, as in the Cetacea and Sirenia. In the seals the flexibility of the digits is greater, as their line of aquatic ancestors is shorter. They add an especial peculiarity in the superior size of the internal digit of the fore foot, and of the internal

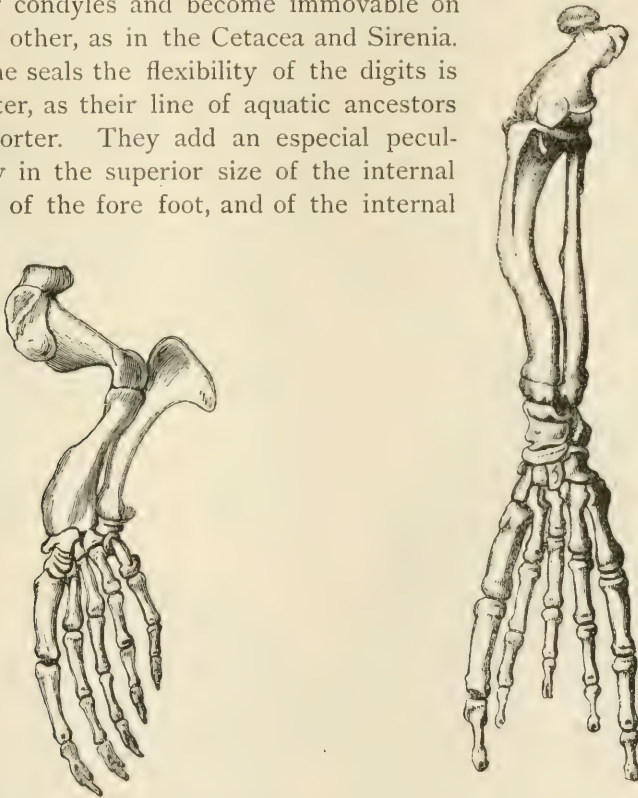


Figure 7.—Anterior and posterior legs of the seal *Monachus albiventer*; from Cuvier.

and external digits of the hind foot. This must be ascribed to the strains incident on use, and the consequent increased nutrition of the parts. Seals constantly rest on shore and on ice-floes, in a manner unknown to both Sirenia and Cetacea. The in-



ternal digit of the manus is necessarily the support of the body when in the act of climbing out of the water and is used in such progress as they make when on the shore. The hind feet are used in the same way; but I must note here, that I do not know to what use the external digit is put which shall account for its superior development. Observation on the living animal only can furnish the explanation.

In the heavy Ungulata the longitudinal diameter of the phalanges is greatly reduced in relation to their transverse. The successive increase in depression in the bones of the feet with the advance of time is to be most readily seen in the order Amblypoda, where we pass from *Pantolambda* to *Coryphodon* and *Uintatherium* (Fig. 8). A similar successive reduction is

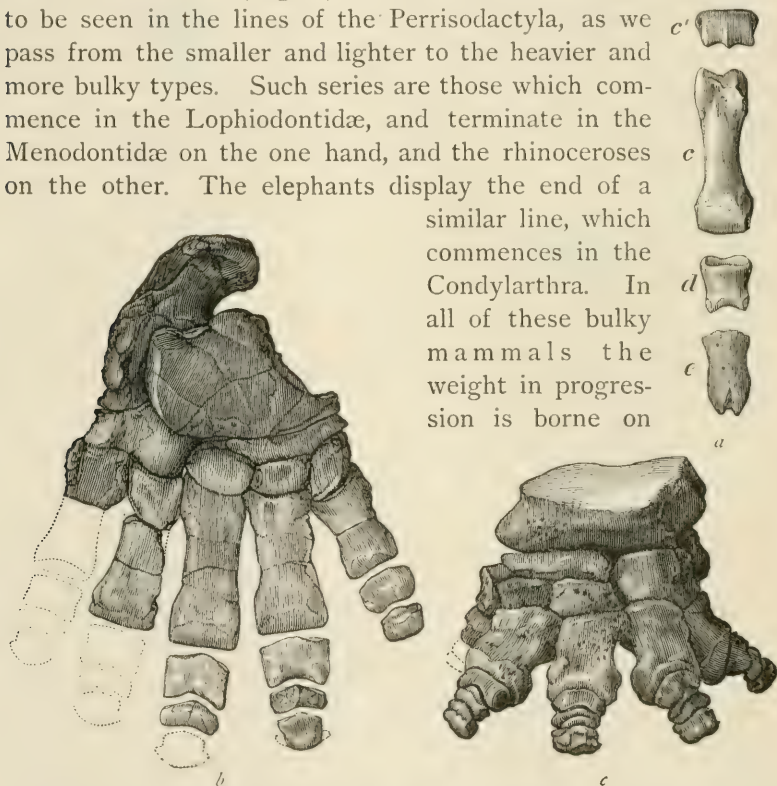


Figure 8. — *a*, *Pantolambda bathmodon*, digit of posterior foot. *b*, Right posterior foot of a species of *Coryphodon* from New Mexico, one-half nat. size. From Report Expl. W. of 100th Mer., G. M. Wheeler, IV., Pl. LIX. *c*, *Uintatherium mirabile*, right posterior foot; from Marsh, *Dinocerata*.

the extremities of the metapodial bones, and the phalanges take but little share in it. They are turned forwards and are nearly useless. Their great reduction in dimensions in these forms appears to me to have followed disuse, and this is then the probable cause of it.

## 2. THE NUMBER OF THE DIGITS.

The reduction in the number of toes is supposed to be due to the elongation of those which receive the greater number of strains and impacts in rapid progression, and the complementary loss of material available for the growth of those not subject to this stimulus. This is rendered probable from the fact that the types with reduced digits are dwellers on dry land, and those that have more numerous digits are inhabitants of swamps and mud, or are more or less aquatic. That this inequality is due to these mechanical causes is still further indicated by the fact that in those forms where the soles are thickly padded (Carnivora, Proboscidea) the reduction has either not taken place, or has made little progress, amounting to the loss of only one digit. (An apparent exception in the case of the camels will be mentioned

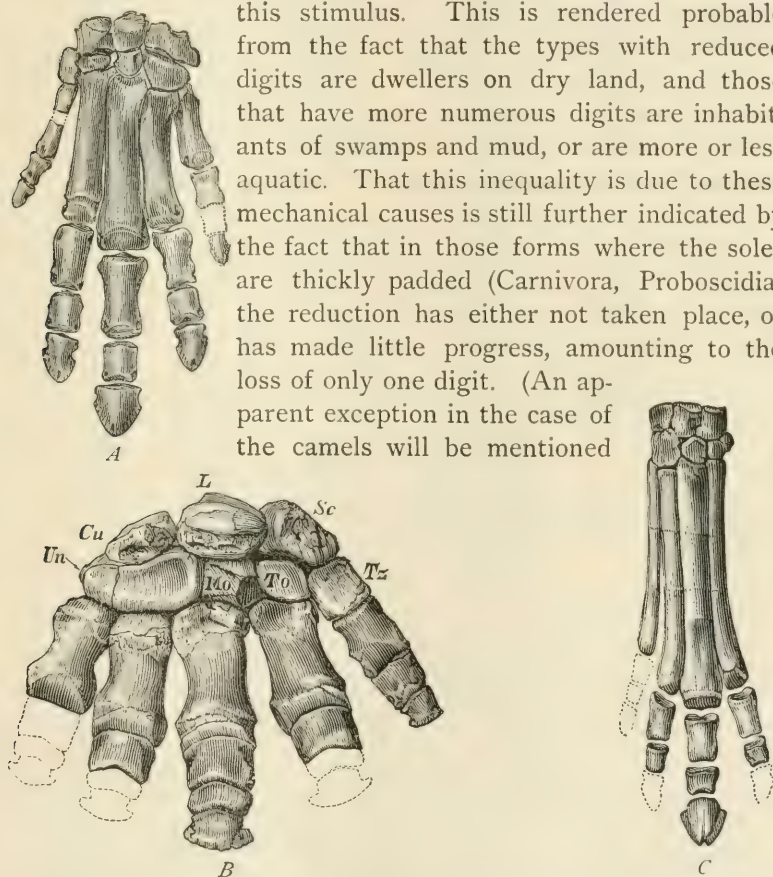


Figure 9.—Anterior feet of primitive Ungulata, reduced. A, *Phenacodus pri-mævus*. B, *Coryphodon elephantopus*. C, *Hyracotherium venticolum*.

later.) A still more important body of evidence which shows that the inequality in size and number of digits is due to impacts and strains unequally distributed, has been brought forward by Ryder. He points out that definite results are to be observed in those limbs of a given type of animal which expe-

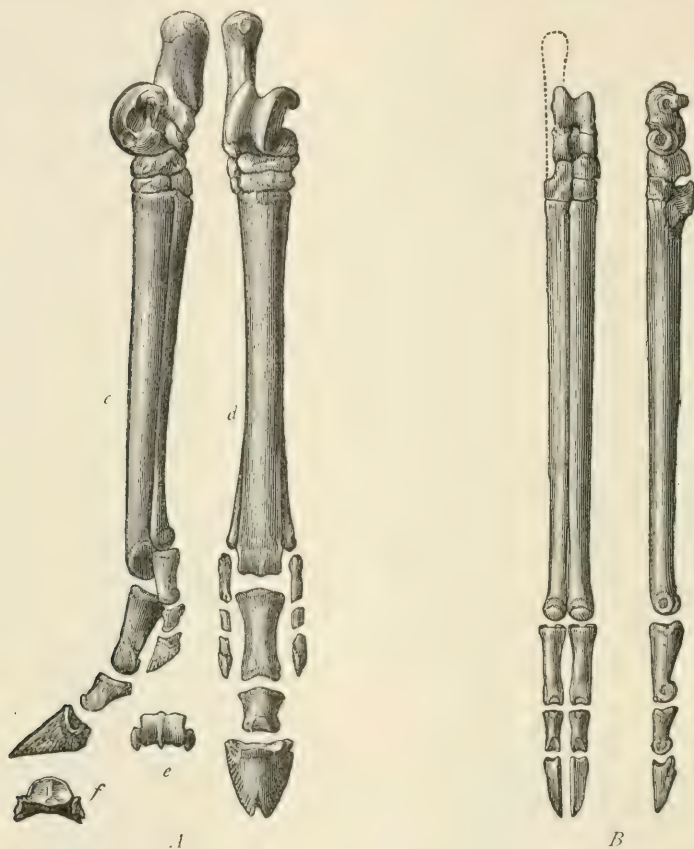


Figure 10.—A, Right posterior foot of *Protolippus sejunctus* Cope, from Colorado, about one-half nat. size. From U. S. Geol. Surv. Terrs., F. V. Hayden, IV. B, Right posterior foot of *Poebrotherium labiatum* Cope, from Colorado, three-fifths nat. size. From Hayden's Report, IV., Pl. CXV.

rience correspondingly definite influences; while in the limbs where the strains are equal, the modifications do not appear. Examples of this kind are to be found in the unguliculate Mammalia, and in the Marsupialia. Thus in the jerboas which use the hind limbs in leaping, these only display reduced digits, the

fore limbs remaining of primitive character. The same is true of the kangaroos. In digging genera the fore limbs experience the modifications, while the hind limbs are more normal, as in *Chrysochloris* and various *Edentata*.

Ryder sums up the evidence in two propositions as follows:<sup>1</sup>—

“I. The mechanical force used in locomotion during the struggle for existence has determined the digits which are now performing the pedal function in such groups as have undergone digital reduction.

“II. When the distribution of mechanical strains has been alike upon all the digits of the manus or of the pes, or both, they have remained in a state of approximate uniformity of development.”

The application of the impact, or strain, or both, in progression, is easily understood. In recover (see p. 166), the leg is bent on the foot as it rests on the ground, and those digits which then leave the ground last, sustain greater strain than those which leave it sooner. In replacing the foot on the ground (plantation), those digits which strike it first, experience greater force of impact than those which strike it later. Supposing the five primitive digits to have been of equal length, the distribution of the impact and of the strain will depend on the angle at which the foot is directed with reference to the direction of motion. If the feet are pointed forwards, the middle digits will experience strain and impact; if outwards, the inner digits bear the weight; if inwards, the external digits receive it.

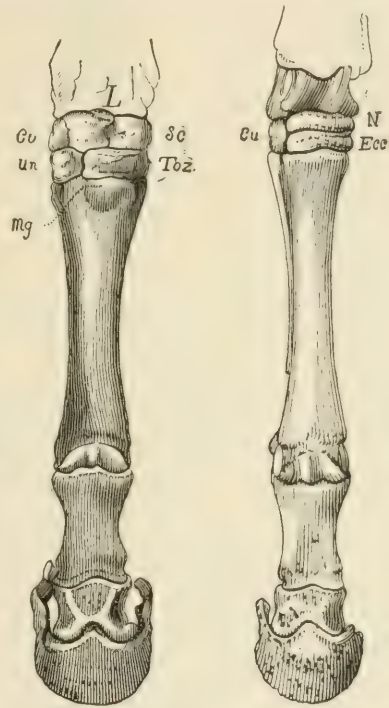


Figure 11.—*Equus caballus*, fore and hind feet; from Cuvier.

<sup>1</sup> *American Naturalist*, 1877 (Oct.), p. 607.



Observation on five-toed plantigrade Mammals shows that their feet are turned neither inwards nor outwards in progression, but straight forwards. It is probable that the primitive *Mammalia* moved in the same manner. This is also to be inferred from the fact that they were plantigrade, so that the leverage transversely in or out which results from the elevated heel of the digitigrade leg was wanting to them. In progression of this type the middle digits of course leave the ground last, and strike it first. Thus the middle toes have been stimulated at the expense of the lateral ones, so that in the *Diplarthra*, either the middle one (*Perissodactyla*) alone remains, or the middle two (*Artiodactyla*). In the kangaroos, the external toes have been chiefly used, so that the fourth and fifth digits have been principally developed. In man, who now turns his feet out when using them as bases of resistance to muscular labor, the inner digit has become most robust. The mechanical history of the human great toe is however yet unknown.

As regards the equal development of the third and fourth digits in the *Artiodactyla*, as distinguished from the development of the middle digit of the *Perissodactyla*, I have advanced the following hypothesis. I have supposed that the primitive members of this former division sprung from pentadactyl plantigrades who dwelt in swamps and walked on very soft ground. The effect of progression in mud is to spread the toes equally in all directions and on each side of the median line. Such feet remain in the mud-loving hippopotamus, and to a lesser degree in the true pigs. From such ancestry the cloven-footed *Diplarthra* derived their characters. The *Hyracotheriinae*, the ancestors of all *Perissodactyla*, display on the other hand evidence of a life on harder ground, especially in the posterior foot, where articulations are already rigidly defined, and the third digit is longer than the others. Some of their descendants love swamps, as one or two species of tapirs and rhinoceroses, but others live on the driest ground, as the Andean tapir, and the African rhinoceros. As to the highest members of both even and odd toed groups, the *Bovidae* and the *Equidae*, their habitat is in the vast majority of cases the dry land (Fig. 12).

Continued and excessive prehensile strain with weight on the longest digits, must be assigned as the cause of the especial elongation; and disuse as the cause of the loss of the

external and shorter digits, of the sloths; so that there remain but two and three (*Cholæpus* and *Bradypus*), and in the climbing anteater (*Cycloturus*) but one principal toe, and two rudiments.

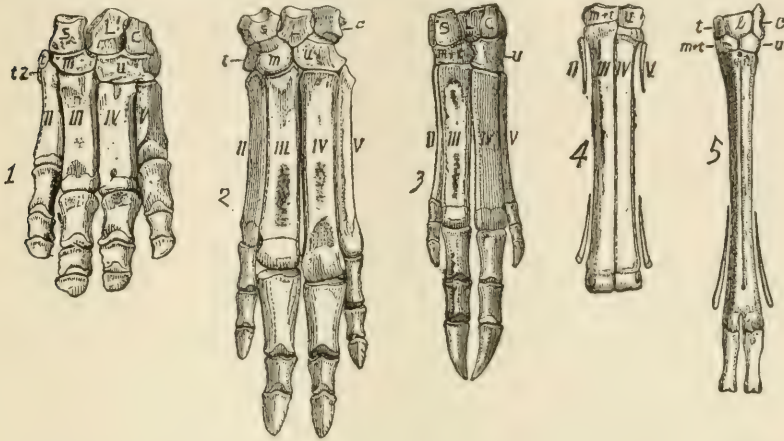


Figure 12.—Manus of Artiodactyla, much reduced; from Kowalevsky. 1, *Hippopotamus*; 2, *Hyopotamus*; 3, *Sus*; 4, *Gelocus*; 5, *Cervus*.

The excessive strain and impact experienced by certain digits in leaping, accounts for the digital reduction in the hinder foot of the kangaroos and jerboas, precisely as in the *Perissodactyle* ungulates.

### 3. THE FIXED ARTICULATIONS.

On entering the subject of the articulations, a preliminary observation on their origin must be made. No evolutionist can doubt that the discontinuity of matter, expressed by an articulation, is due to flexure of the body exhibiting it. Primitively, the softer tissues of which all animals were composed, as the inferior forms are to-day, were susceptible of flexure in various directions. The deposit of hard mineral or organic substances within the tissues, producing calcareous layers, chitin, horn, and bone, has not in a majority of cases suppressed motion, but has restricted it to definite directions. It cannot have been otherwise than that, since the motions of animals continued during the evolution of their hard parts, these hard parts grew in exact adaptation to these movements. Thus at the points of greatest flexure joints would be formed, and between these joints the deposit would be continuous.

The fixed articulations are not absolutely without movement, because termed fixed. When two adjacent bones become entirely motionless through the fixity of their positions, they are apt to coössify, especially if growth be stimulated by impact of the parts. Such a case is the confluence of the cuboid and navicular bones in the Bovidæ and Equidæ, and the fusion of the cuneiforms in some of the former. Such are the fusion of the magnum and unciform in the manus of the Cycloturus, and of the trapezoides and magnum in Bradypus. Such the union of the metapodials in both extremities of the three-toed sloth. The fusion of the scaphoid and lunar bones in the Carnivora is not so readily explained. It may be, however, traced to a strain similar to that experienced by the feet of sloths, Cycloturus, etc., but for a different purpose, that of seizing and rending prey. But this suggestion may be worthless, and it does not offer any demonstration as to how such strains should produce such result.

The fixed articulations are those between the carpal and tarsal bones, and those between these and the metapodials. In the Diplarthra another fixed articulation is that between the ulna and radius, and in this and other orders, that between the tibia and fibula.

*a. The Ulna and Radius.*

The relation of the head of the radius to the ulna is, in lower land vertebrates, a more or less loose one. In the lower Mammalia the head is generally oval, permitting of greater or less supination of the manus. In the higher Edentata and Taxeopoda, the head becomes round, permitting perfect supination in the great anteater, the monkeys, and man. In the Ungulata its development is in the opposite direction or towards fixity. It becomes flatter, and incapable of movement; and, finally, in the Artiodactyla, it is firmly articulated with the ulna by a coarse peg and notch, or gomphosis, followed by coössification in the Camelidæ. It is evident that the rotundity of the head of the radius has been produced by the more or less successful attempt to rotate it in the act of supinating the manus. The immovable condition seen in the Ungulata is as clearly due to disuse of the supinating function, in a use of the fore limb where such movement is unnecessary. It appears that the impact or concussion of the blow of the ungulate foot on the ground has caused an

expansion of the external border of the head of the radius over the adjacent external part of the ulna. The latter forms, in the Diplarthra, a more or less evident ridge, corresponding with the external condyle of the humerus, while the internal border forms another ridge, which corresponds to the internal condyle of the humerus. These elevations are due to the existence of greater friction, *i.e.* stimulation, in front of convex condyles than is possible at the point of the cotylus which receives the groove of the condyles. A groove of the coronoid surface of the ulna, opposite the groove of the condyles, exists accordingly in most ungulates, since here contact, friction, and impact are at a minimum. The head of the radius fits this groove, which is at first quite shallow, as in the peccary and hog. In the extension of the head of the radius externally, the latter naturally embraces the external ridge of the coronoid surface of the ulna. This embrace, together with the opposite descent of the head of the radius into the median groove, constitute a very strong double open peg and notch, or short tongue and groove, articulation. This is most pronounced in the highest Diplarthra, as the crests of the ulna tend to become more elevated under the influence of the impacts and friction conveyed to them through the convex parts of the humeral condyles. This articulation, like all those of the Diplarthra, is a protection against dislocation from lateral strains and blows. For an explanation of the origin of the elbow joint, see page 179 (Plate I.).

β. *The Carpus and Tarsus.*

The conversion of a taxepod into a diplarthrous ungulate has been accomplished by the rotation outwards of the lower leg with the first row of the carpus and tarsus, on the second row; or else by the rotation inwards of the second row on the first, in both the fore and hind feet. The question to be solved here is, which row has moved from its primitive relation, or in what direction has the energy of rotation been applied. After long and careful observation of the locomotion of living Mammalia, and especially Diplarthra, I have reached the following definite conclusions:—

In locomotion each foot occupies two relations to the act. The first is the setting-down of the foot, or *plantation*; the other is the lifting of the foot from the ground, or *recovery*, to



use the nomenclature of Dr. H. Allen. In plantation, plantigrade mammals do not turn the toes outwards; while digitigrade forms do turn them out. This may be readily observed in

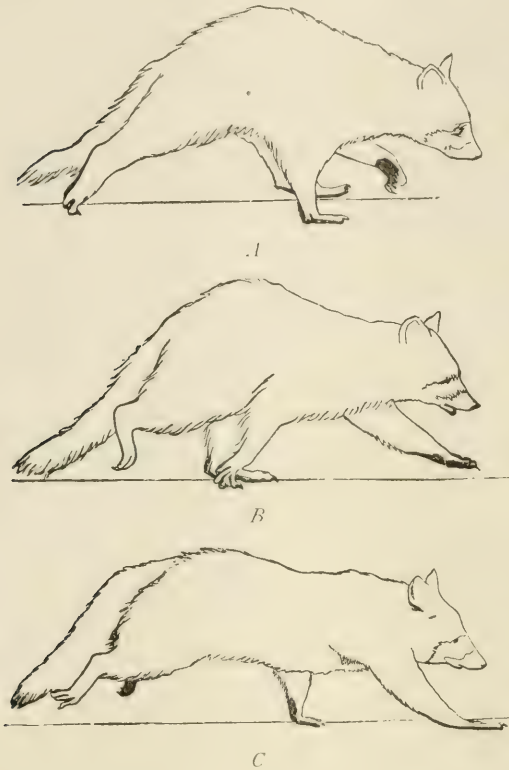


Figure 13. — *Procyon lotor*, gaits; from Muybridge, Animal Motion. *A* shows semisupination of the left manus and lever strain on right pes in recovery; *B*, lever strain on recovery of right manus, and plantation of left pes; *C*, plantation of left manus.

*be* forwards and inwards, or forwards and outwards. In recovery, the twist is greater in a long than in a short limb. In the language of mechanics, the length of the arc of torsion is directly as the length of the limb. It is probable that it is for this reason that the digitigrade forms turn the toes out in plantation also, the structure having adapted itself to this motion, so as to perform antero-external rotation most easily.<sup>1</sup> In

anterior and posterior views of most of the Diparthra in motion, and especially in Artiodactyla. In plantation, the elbows and hocks rotate inwards, and the toes outwards. In recovery, this rotation is necessarily continued. As the body passes the position of the stationary limb and foot, it gives to the latter a slight twist outwards and forwards, in answer to which the foot is lifted from the ground, or recovered. At recovery, the rotation *cannot* be in any other direction in any mammal; in plantation, it *may*

<sup>1</sup> I have made these observations on various species of Auchenia, Camelus, Antilocapra, Antelope, Capra, Bos and Cervus, and in Tapirus, Rhinocerus and Equus,

Figure 14. — *Gazella dorcas*, gazelle; from the Standard Natural History.



plantation, the rotation of the foot is arrested at the moment of contact with the ground, with the result of producing a torsion of the segments of the limb on each other. The energy of the

torsion is directly as the distance from the moving body, since its cause resides in the inertia of the free hoof, which is that of the animal of which it is a part.

The mechanical effect of this torsion is seen at various points on the length of the limb. In the fore limb (I.) the distal extremity of the radius has spread outwards so as to cover almost the entire carpal articulation, and the ulna has been excluded from it. That torsion with impact is the correct explanation of this divergence from the condition of lower land vertebrates is rendered probable by the large ulnar carpal articulation in primitive plantigrade types with taxepodous carpus, as *Elephas*, *Hyrax*, and *Phenacodus*. II. The lines of mutual contact

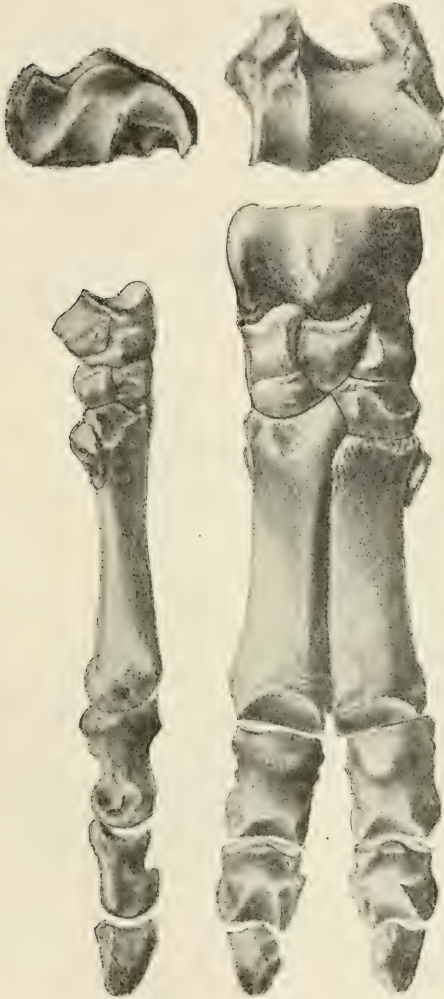


Figure 15.—*Boöcherus humerosus*, Cope; distal extremity of radius, showing oblique intercarpal keels; do. of humerus; also left fore foot from front and from inside; one-fifth nat. size.

in the zoölogical garden of Philadelphia. The horse turns the toes out but little, and frequently turns them in; but the tapir, which represents the horse's ancestors, turns them out. The llama also turns the hind toes out very little, or not at all.



of the carpal bones of the first row have become oblique, outwards and forwards, in the Artiodactyla, except the Camelidæ; and hence the intercarpal crests of the radius have become oblique in the same way. III. The bones of the first carpal row have come to occupy the positions above the lines of separation between those of the second row, thus producing diplarthrism.

IV. The bones of the first carpal row have moved to a position external to the axial lines of their corresponding digits (*e.g.* the lunar is external to the axis of the third metapodial in Perissodactyla (Fig. 16) and Artiodactyla (Figs. 12-15), instead of above it as in Taxeopoda (Fig. 16).

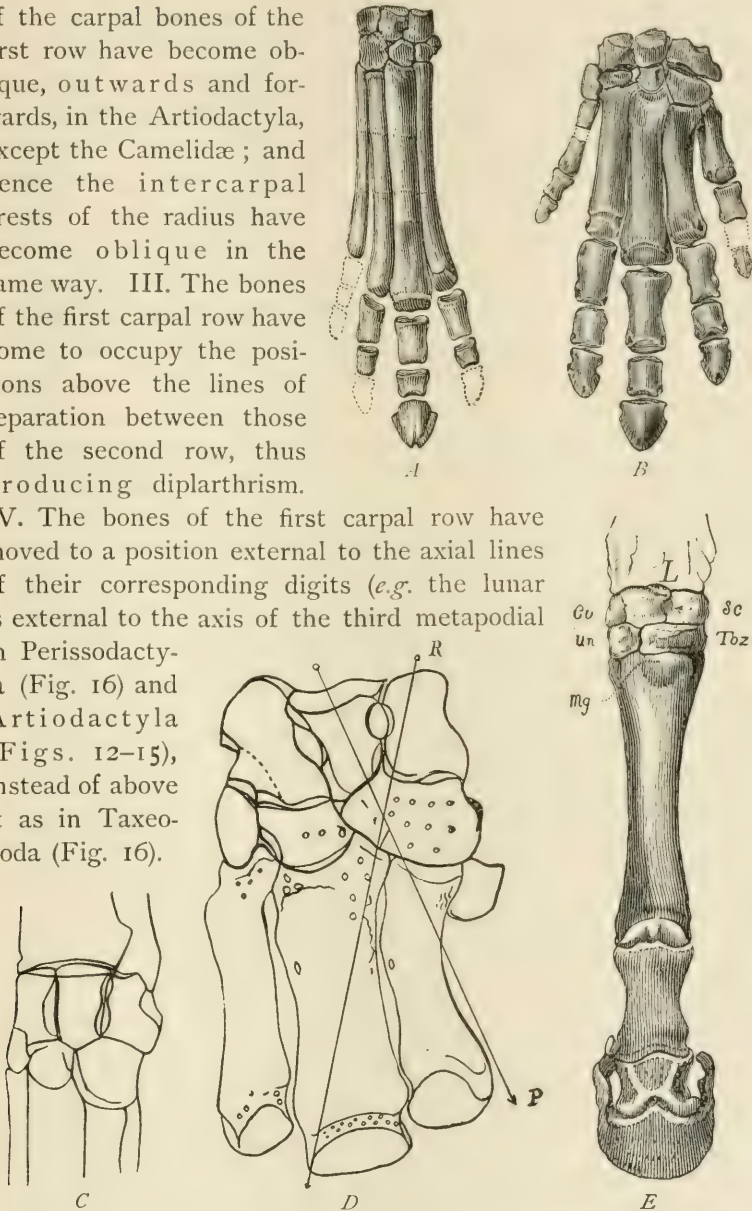


Figure 16. — Manus of Phenacodus (A) and Perissodactyla; viz.: B. *Hyracotherium venticolum*; C. *Hyrachyus agrestis*; D. *Rhinocerus unicornis*; E. *Equus caballus*; all showing external transposition of os lunare, L. P. Line of strain in plantation; R. Do. in recover.



In the hind leg similar phenomena are exhibited. I. The fibula has been almost entirely excluded from the tibio-tarsal articulation. II. In some forms (the equine line) the tibio-astragalar tongue-and-groove joint has become oblique outwards and forwards. III. The astragalus (of the first tarsal row) has extended its distal articular surface on the cuboid (of the second row), so as to exclude more and more the calcaneum.

That these changes, so remarkably similar in all of the articulations of the legs, have resulted from the torsion in question, is rendered highly probable by the fact that they have appeared in all lines of descent, except that of the Amblypoda, in direct ratio to the advance of digitigradism in the Ungulata, and the measure of the one is a measure of the other.

The movement involved in the preceding discussion is that of plantation. In recovery, we meet with another element in the problem. In spite of the outward rotation of the bones of the first carpal and tarsal rows, the bones of the second row have not moved outwards on the metapodials. They have remained stationary as regards the axis of support, while the *metapodials* have been evidently pressed outwards. This is seen in two points. First, the external bone of the second row, the unciform, is in all Diplarthra much extended inwards. It reaches contact with the middle bone of the first row (the lunar) before the internal bone of the first row, the scaphoid, has extended outwards beyond the trapezoides to the magnum. This is the permanent state of affairs in the Amblypoda (Fig. 9). Second, the metapodial bones abut with the external sides of their proximal extremities against inner distal facets of the second row of tarsals. This must have been brought about by an inward movement of the second row of tarsal bones, or by an outward movement of the metapodials to meet them. The direct effect of the arrest of outward torsion of the foot is to 'dislocate the tarso-metatarsal and carpo-metacarpal articulations, unless some antagonistic movement prevent it.

A strain antagonistic to the external movement of the tarsal bones is introduced at the moment of recover of the foot. Dr. H. Allen shows in his exposition of the Muybridge photographs, that in approaching the recover, the weight supported by the foot is transferred to its inner border, a movement which necessarily throws the strain on the external sides of the heads of

the metapodials. Hence the apparent outward movement of the latter. The structure, however, represents an inward pressure of the second row of carpal and tarsal bones on them. The bones of the second row are then subject in locomotion to two influences which tend to shift them from their position. First, the pressure outwards on plantation, derived from the weight borne by the leg, and resisted by the metapodials on the ground; and second, pressure inwards of the weight, on its transfer to the inner side of the foot, also resisted by the metapodials on the ground on recovery. The weight is the same in both cases, and there is no reason to doubt the equal velocity of the two strains. Hence the effect of the one is neutralized by the other, and the bones of the second row retain their position.<sup>1</sup>

It is obvious that in the beginning of the rotation of the first on the second row of carpals and tarsals, of a taxeopodous mammal (Fig. 16), the inferior bounding angles of the former would be arrested by the superior bounding angles of the latter, especially if there should be any play of longitudinal motion of the digits and carpal and tarsal bones resting on them. Such play there would be in a taxeopodous foot. This arrest would flatten the opposing angles and produce planes or facets, and diplarthrism would have its beginning. The angles separating these planes would penetrate deeper into the fissures separating the bones under the influence of concussions. (See carpus of *Boöchærus*, Fig. 15.) In some instances, as in the *Oreodontidæ*, some *Tragulidæ*, and *Elotherium*, the lunar has penetrated so far as to almost divide the second row of carpals.

An important result of the outward movement of the bones of the first carpal and tarsal rows has been to leave unsupported the internal element of the second row, the trapezium and the entocuneiform. As a consequence of this, these elements come to have a mere lateral attachment, which is not favorable to the rigidity of the pollex and hallux which are attached to them. This condition leads to disuse, which the strain of the inner side of the foot in recover is not sufficient to overcome. The external digit of each foot, on the contrary, remains, since its

<sup>1</sup> In my original discussion of diplarthrism (*American Naturalist*, Dec., 1888), I omitted to consider the history of the second row of carpals and tarsals. This deficiency is now supplied. I have been guided to the explanation by Dr. H. Allen's observations on p. 50 of his exposition of the Muybridge photographs.

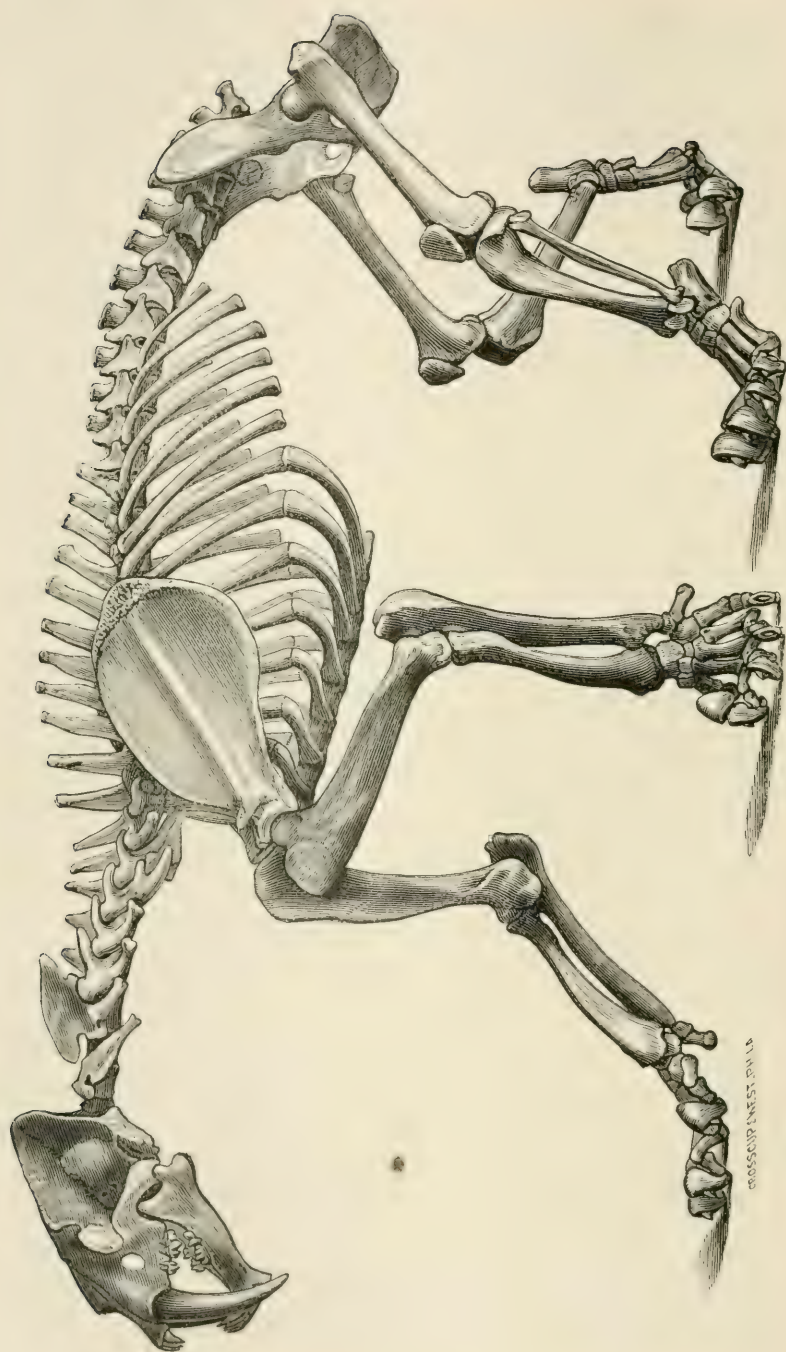


Figure 17. — *Smilodon neogaeus* Lund, from the Pampean formation of Buenos Ayres: after Burmeister.

connection with the carpus and tarsus is maintained. In the developed taxepodous posterior foot, on the contrary, the hallux remains for a much longer time, as in Carnivora; and where it has been especially used in prehension, as in *Quadrumana*, it becomes enlarged. In man it receives especial strain in recover, particularly in those men who turn out the feet in walking. To this cause we may ascribe the gradual increase in size of this digit, until in the highest races it exceeds the second digit in length.

The above reasoning when applied to the Unguiculate series is modified by the existence of other conditions. In the Carnivora the weight of the body does not rest on the unguis as in the Ungulata, but on the pads of connective tissue beneath the digits. Consequently, on the application of the foot to the ground, the distal bones in the carpal and tarsal articulations do not present the rigid resistance seen in the Ungulata, but yield more or less to the torsion. Hence, no alternation of these bones takes place in the hind foot of the Carnivora, where the eversion of the digits is moderate. In the case of the fore foot, the eversion and consequent torsion are so much greater, that the alternation is produced (Figs. 17, 18). In the plantigrade bear the alternation is almost nil.

It may be here objected that the camel walks upon elastic pads as do the Carnivora, and yet the alternation has really taken place. It is on this account (as I have maintained) that the distal metapodial tongue keels were never completed in these animals. But if the camel does not rest on the unguis with sufficient fixity to resist torsion, thus resembling in some degree the Carnivora, the ancestors of the camels, the *Poebrotheriidae*, resembled other *Diplarthra* in this respect. As already pointed out, their foot structures were like that of other *Artiodactyla*, the palmar and solar pads of their descendants are of comparatively modern origin. Their *diplarthrous* structure is inherited.

The carpus of the *Anthropomorpha* and *Quadrumana* present some interesting modifications. In most of the genera the arrangement is taxepodous, but in the *Simiidae* the scaphoides extends somewhat outwards over the magnum, and the lunar completely overlaps the cuneiform (Fig. 19). In man (Fig. 2) the lunar extends externally over the cuneiform, and the scaphoides rests partly on the magnum, giving an arrangement similar to





Figure 18. — *Hyena striata*, striped hyena, showing position of feet; from the Standard Natural History.

that of the Diplarthra, but of inferior fixity. In the baboons (*Cynocephalus*) the relations of the lunar and unciform are as in man, while the scaphoides through the centrale, which has a strong lateral facet for the magnum, rests entirely on the trapezoides, thus approximating the arrangement in the Amblypoda. In Anthropomorpha the metacarpals are nearly in line with the carpals of the second row, inclining, however, to articulate in addition with the carpal to the *inner* side of them, contrary to the arrangement in other Mammalia. This disposition is little marked, however, being restricted mainly to the fourth metacarpal, which has more or less contact with the os magnum.

The relation of the form of the bones of the manus to their uses is obvious in this order. The Simiidæ use the fore limb as a suspensor, as they swing from branch to branch of the forests in which they live. The swing of the body on the arm is divided into two parts, in which the strains are opposites of each other, as to the metacarpal, but identical as to the cubito-carpal articulations. The change of relation to the point of suspension when swinging from one place to another, is permitted by the rotation of the manus and radius round their long axis, so that an act of supination is performed. The strain on the proximal carpal bones by the radius is then outwards, which accounts for the external extension of the scaphoides over the magnum. The lunar also is carried by the same strain far external to its usual position, entirely covering the cuneiform. The latter and the unciform are small, and the cuneiform is comparatively unimportant. This restriction of the two elements of the external row of the carpus is to be accounted for on the ground of disuse. The weight is principally supported by the scaphoides and lunar, and the strain passes exclusively through them as they only are grasped by the fore arm, *i.e.* by the radius. The ulna has either very slight or no contact with the cuneiform, serving merely as the point of suspension round which the radius and hand rotate. The relation of the fore-arm to progression is quite the reverse of that seen in the Ungulata, where it sustains so much impact and strain. The metacarpal-carpal articulation is not modified. In approaching the position below the point of suspension, the strain of the weight is outwards from the fixed point. This presses the heads of the metacarpals inwards on the carpus, and the segments proximal



to the former, outwards on each other. Beyond the point of vertical suspension the strain on the heads of the metacarpals presses them outwards, thus antagonizing the effect of the inward pressure. The linear relation therefore remains unaltered.

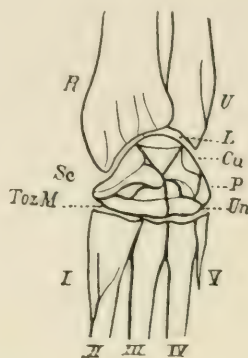
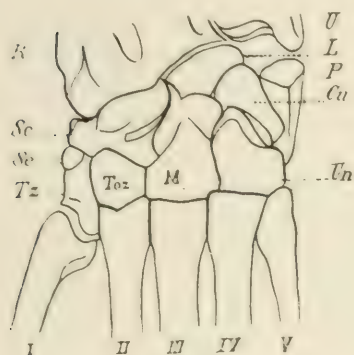


Figure 19. — *Simia nigra*, carpus one-fourth the nat. size.

Figure 20. — *Bradypus tridactylus*, carpus one-fourth nat. size.

In the sloth (*Bradypus tridactylus*), which also progresses in suspension, the rotation of the radius and manus is far less considerable than in *Simia*; is in fact almost wanting. In progression the strains are alternately opposite each other at the cubito-carpal articulation, and as a consequence the scaphoid and cuneiform are subequally developed and at the expense of the distal part of the lunar. The equality of these opposed strains is also represented by the similarity of the articular surfaces between the scaphoid and trapezoido-magnum, and the cuneiform and unciform (Fig. 20).

I can offer no plausible theory to account for the diarthry of the human carpus. The movements of the human hand are so many and various that the explanation of its carpal structure is a most complex proposition (Fig. 1 B, p. 150).

An especial peculiarity characterizes the cubito-carpal and intercarpal articulations of the Anthropomorpha, Quadrumana, and sloths. Both of these articulations are strongly convex proximally, offering halves of ball and socket joints. In the intercarpal articulation the articular surface covers a large anterior face of the magnum and unciform bones. This form is represented by a trace only in Ungulates. Its function evi-

dently is the inward flexion of the manus, and it is especially characteristic of forms which suspend themselves by the fore limbs, as above pointed out. It is not difficult to perceive in this instance how the function has produced the structure by use. Continued flexion and extension has rounded the angles, especially on the dorsal side of the carpus, and the stimulation has elongated the elements in the direction of greatest pulling strain; *i.e.* longitudinally (Fig. 20). This is in great contrast to the flatness, both transversely and anteroposteriorly, seen in Artiodactyla and horses, where the parts have been subjected to impact from hard earth for so long a period.

Some apparent exceptions to the above general principles must be now referred to. The genera Hyrax and Dendrohyrax are closely allied, yet the one displays a taxepod, and the latter a diplarthrous tarsal structure (Osborn). A preparation for the latter is seen in some Periptychidæ, and in some Carnivora, as Ursus and Mustelidæ, in the extent of the contact of the condyle of the head of the astragalus with the cuboid, without the production of a facet on either. This facet could be, however, easily produced by the simple flattening of the appressed surface by impacts, and this is, it may be supposed, what has taken place in Dendrohyrax. Observations on the movements of the species of this genus in life are necessary to solve this question.

The Amblypoda of the Wasatch and Bridger epochs are distinguished by the great diplarthrism of the tarsus, although they are plantigrade and pentadactyle (Figs. 8-10). In this order, as already indicated, the feet have shortened with the advance of time; and though it is hardly probable that they have descended from a digitigrade type, their ancestor, Pantolambda, was much more capable of varied movements than they. The history of this line must be better known before any reasonable explanation of the character of the hind foot can be reached.

#### 4. THE GINGLYMOID ARTICULATIONS.

The mobility of the ginglymoid articulation depends on its combination of convex with concave surfaces, which permit flexion and extension of one bone on another; in other words, they consist of a condyle and an adapted cotylus. The fixed articulations consist, on the other hand, of adapted faces, which



do not admit of flexion and extension of the elements thus connected. A transition from a ginglymoid to a fixed articulation is seen in the modification of a Condylarthrous convex distal articular surface of the astragalus into the fixed or faceted distal articular surface of the Perissodactyla (Figs. 21-22c).

Another modification of the Condylarthrous astragal surface is that seen in the Artiodactyla. Here the mobility continues, but it is divided into two condylar faces which necessarily permit motion in one direction only. It appears easy to account for the modifications of the Condylarthrous astragalus into that of the two orders mentioned,



FIG. 21.

Figure 21. — *Phenacodus primævus*, carpus and tarsus; *a*, carpus, proximal view, first row; *b*, do. second row; *c*, tarsus, distal view of astragalus and calcaneum; *d*, proximal view of second row of tarsals.

Figure 22. — *Hyrcacotherium venticolum*, posterior foot: *a*, left side; *b*, front; *c*, distal view of astragalus and calcaneum.

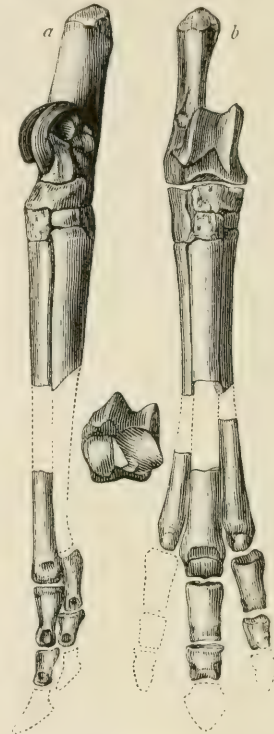


FIG. 22.

Mammalia with soft pads on the feet, this chance does not occur; as Carnivora, Proboscidea, etc.

The movable or ginglymoid joints of the limbs are either simple or trochlear. The former are the proximal extremities of the humerus and femur, and the distal extremity of the astragalus in all except Diplarthra. The trochlear are enumerated further on. That they all originated from the simple ginglymi is shown

by paleontology. The elbow joint passes from simple to trochlear, from the lower or less specialized Mammalia to the most specialized. Nowhere is the direct mechanical effect of motion more demonstrably evident than in the movable articulations of the skeleton of the Mammalia.

*a. The heads of the humerus and femur* represent smaller and larger segments of spheroids, and both look in part upwards. These articulations are not due to impact, but to rotary movement of the movable limb element on the fixed scapular and pelvic arches. This movement antedates in time the existence of impact, since it characterizes the movements of aquatic animals which preceded the terrestrial. Neither of these articulations acquired their spheroidal form until the advent of the Mammalia. To the more constant and uniform activity of the Mammalia, as compared with their reptilian ancestry, must we ascribe the gradual rounding of the humeral and femoral heads, which form the most nearly universal joints in their skeleton.

*b. The Elbow Joint.* In lower salamanders, as *Cryptobranchus*, the ulna and radius rest normally, like the tibia and fibula, in the transverse plane of the distal extremity of the humerus. In terrestrial *Batrachia* and *Reptilia* (*Theromora*, *Lacertilia*), the plane of the ulna and radius is either oblique or at right angles to that of the distal extremity of the humerus. Mammalia possess the same character, the radius resting proximally above or anterior to the ulna, instead of alongside of it as in the lower *Batrachia*. This position may be ascribed, I think, to the long-continued action of the supinator muscles of the forearm, together with that of the biceps flexor, in the endeavor to use the fore feet for purposes other than mere locomotion. Supination and flexion of the fore arm are necessary for any use of the manus in connection with the head, or in order to grasp any object which should project in front of it. In both reptiles and mammals the condyle of the humerus is divided by a shallow vertical groove; that is, a groove in the line of the long axis of the leg. This groove is due to the fact that when the ulna and radius assume a relation transverse to the end of the humerus, their transverse diameter, especially that of the ulna, is less than the latter. The groove or median concavity is then nothing more than the result of the pressure and impact of the narrower ulna on the middle of the condyle, experienced during

active use. It results, also, in the lower Mammalia that the humeral condyles project beyond the ulna and radius on each side. The torsion experienced by the limb at the moment of contact of the foot with the ground, produces a pressure of the inner end of the condyle forwards and outwards against the corresponding part of the ulna, and radius if it extend so far inwards. The external part of the humeral condyle is correspondingly pressed backwards. The result is a flare of the inner anterior and posterior external edges of both the condyle and cotylus, if there be any free margin to either. Hence the obliquity of the ulnar cotylus in Mammalia, whose locomotion is on the ground. Those which, like the Anthropoid apes, swing themselves from branch to branch of trees, experience alternate torsions of the fore leg in both directions. Hence the edges of the ulnar cotylus are flared equally in both directions precisely as the strain on the material requires (Plate I. Fig. B). To this torsion we can ascribe also the development of a flange on the inner anterior edge of the humeral condyle, in Condylarthra and Unguiculata in general, and the corresponding oblique truncation of the adjacent edge of the head of the radius, and the posterior flange of the cotylus of the ulna on the external side. The humerus forms no flange on the external side, because it does not overhang the ulna sufficiently; the ulna being itself the external bone of the fore arm. Where the humerus does not overhang the inner side, as in Hyrax, there is no flange of the former, and no truncation of the head of the radius on the inner edge (Plate I. Fig. E).

In the lines of the Unguiculates, of the Edentates, and of the Taxeopoda, there is an additional development of the power of the supination of the manus. This is accomplished by the rotation of the distal and of the radius round that of the ulna, and the rotation of the head of the radius on its own axis. So the head of the radius becomes more and more round, in consequence of the mechanical constriction of its long axis, till in the great anteater, the sloth, and the monkeys, it is perfectly round, and rotates in its ligamentous ring, while maintaining its position on the front of the ulna. In both of these types it lies on the external side of the middle line, owing to the habit of supination, which throws the radius more and more outwards. Perhaps it is for this reason also that the ulna extends inwards proximally, so as to permit of no internal humeral flange in both forms.

The notch between the head of the radius and the coronoid process of the ulna is fitted by a corresponding ridge of the humeral condyle, the intertrochlear crest, in the *Anthropomorpha*. In the *Myrmecophagidæ* it is wanting, because the median convexity of the ulnar cotylus is opposite the space between the head of the radius and the coronoid process, so that the ulnar concavity of the humeral condyle is immediately continuous with the radial surface of the same.

In the elbow joint of the *Diplarthra* a different state of affairs exists. The head of the radius lies firmly on the coronoid process of the ulna, having the transverse diameter increased. This increase of width I suppose to be caused by the strong impact of the condyles of the humerus directly upon its extremity, which accompanies the use of the limb as a support, especially in alighting upon it in the rapid locomotion characteristic of diplarthrous *Ungulata*. The increase in diameter is both external and internal, and so far as to equal the width of the humerus, and not to permit any flange on the edge of its internal condyle. The effect of impact on the head of the radius is greater than it is on the condyles of the humerus, because its energy is expended in the case of the former on a surface whose arc is only one-third that of the latter. It must be remembered, however, that it is not equally distributed on the humeral arc. The coronoid process of the ulna also expands transversely, but not to the same extent as the head of the radius. Its external expansion is overpassed by that of the radius, the external portion of the radius in the *Diplarthra* occupying the position of the entire head of that of man. The effect of the two convexities of the humeral condyles has been in most *Mammalia* to prolong in the direction of their movement the corresponding parts of the coronoid region of the ulna. Hence there has appeared an external and an internal ridge of this part, enclosing a concavity or groove between them. The head of the radius in its external extension has overpassed the external ridge, and embracing it, has formed an interlocking fixed articulation. The interior face of the head of the radius has also applied itself exactly to the median groove of the ulna, forming another fixed key joint of much firmness. The articular face of the head of the radius has naturally formed a ridge in adaptation to this groove of the ulna, as well as to the groove of the humerus which corresponds to it. Opposite



the two crests of the ulna the articular surface of the radius is naturally concave, receiving the convexities of the humeral condyle. The external cotylus has become a groove corresponding to a crest of the humeral condyle, which has been developed by gradual modification of a strong convexity, such as is seen in *Anoplotherium* and *Oreodon*, and the *Condylarthra* (Plate I. Fig. D), and which is characteristic of many *Unguiculata*. Its keel or tongue-like character may be ascribed to the action of torsion combined with impact, as we find to have been the case with the distal metapodial articulations. It has been homologized with the intertrochlear crest of the *Anthropomorpha*, but it is not homologous with it. It is homologous with the external condyle or trochlea, while the crest of the *Anthropomorpha* is really intertrochlear. The condyle is developed extad of this keel, coextensively with the head of the radius. The development of these two extensions is necessarily coextensive, since they are mutually dependent on each other for their growth stimulus. Judging by the character of *Hyracotherium venticolum*,<sup>1</sup> the external extension commences with the head of the radius, since the external condyle of the humerus is much more retreating proximad than it is in the species of *Equus*. It has developed distad in the latter genus, so as to bear nearly the same transverse line as the internal condyle (Plate I. Fig. E).

The mechanical cause of the origin of this peculiar external roller of the distal humeral condyle is the same as that which has given origin to a similar structure on the external sides of the distal extremities of the metapodial bones. This is the excessive use consequent on the very frequently externally divergent relation of the distal to the proximal element in the case; here, of the fore arm on the humerus. This occurs constantly in the most rapid movement of a diplarthrous Ungulate. On alighting on the ground at the end of a leap, the anterior foot supports the entire weight for a shorter or longer time according to the gait, the foot resting below the middle line of the body. According to Allen<sup>2</sup> the foot even crosses the middle line, and rests on the opposite side of that line to which it really belongs. Thus the remainder of the leg is abducted or bent

<sup>1</sup> *Tertiary Vertebrata*, Cope, Pl. XLIX. b, Figs. 2, 3.

<sup>2</sup> *Materials for a Memoir on Animal Locomotion*; from the Report of the Mybridge work at the University of Pennsylvania, 1888, p. 58.

outwards on the humerus, the animal being knock-elbowed in this act. The effect of this position during impact is to extend both radius and humerus outwards, and to push from its primitive position that one of the two elements which has the least longitudinal support (Fig. 23).

The history of the elbow-joint in the Lagomorphous Rodentia is the same as that which I have described in the Diplarthra, excepting that the applied surfaces of the head of the radius and the ulna do not mutually interlock. The expansion of the head of the radius is identical in the two cases, as is the form of the condyles of the humerus, including the trochlear crest and the extension external to it (Fig. 42). This is an admirable illustration of the production of like effects by like causes, in two widely different lines of descent.

The elbow joint of the bat has some points of resemblance to that of the higher Diplarthra and Rodentia. The ulna is reduced to a splint below the proximal part of the radius, to which it is not co-ossified,<sup>1</sup> and the olecranon is represented by a sesamoid bone in the tendon of the extensor muscle. The humeral condyle is developed external to the external convexity, but the internal condyle has no extension beyond the flange, thus differing from Bovidae and Leporidae. In Pteropus and Vespertilio the ulnar groove of the humerus is not deep. In Pteropus the external convexity of the condyle is wide; in Vespertilio it is narrowed into a weak troch-

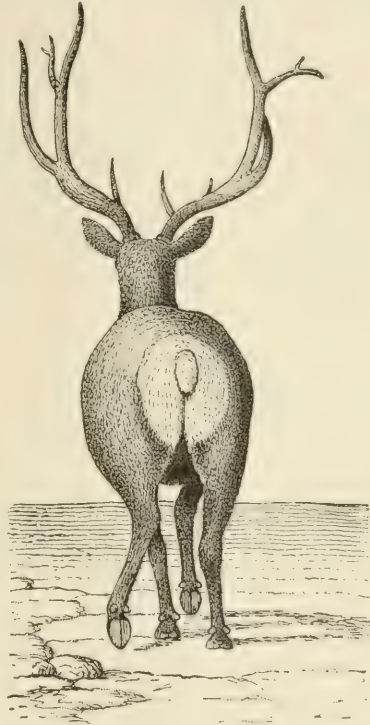


Figure 23. — *Cervus canadensis*, trotting, from behind; from Muybridge, Animal Locomotion; showing position of fore foot in support of the body.

<sup>1</sup> See W. Leche, *Ueber der Entwicklung des Unterarms u. Unterschenkels bei Chiroptera*. K. Svenska Akad. Handlingar, V., 1879.

lear crest. In *Rhinolophus* (Plate I. Fig. C) the trochlear crest is prominent and acute, and the intertrochlear groove is deep. The head of the radius does not extend internally to the external crest of the external condyle, which is here much like the

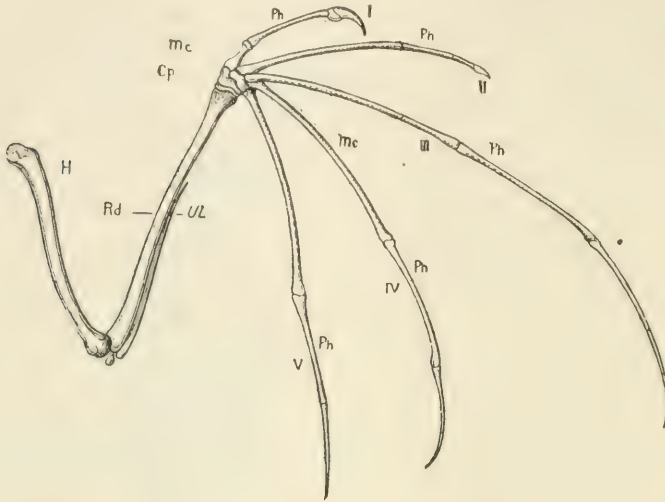


Figure 24. — Anterior limb of bat.

flange of the Carnivora. The high development of this elbow-joint in the Chiroptera cannot of course be ascribed to impacts, but it may be ascribed to an equally effective cause, viz., the great mutual pressure of the parts, accompanied by torsion, when in action. The muscular tension during flight is very great, and inequalities already existing in the surfaces of the bones forming the articulation would tend, under the influence of torsions, to be exaggerated. The external and internal condyles of the humerus were already distinct in the ancestors of the bats, of which *Galeopithecus* may be regarded as the nearest living ally. The pressure of the tendon of the triceps extensor muscle, with its sesamoid bone, has tended to deepen the intertrochlear groove.

The elbow joint of the mole presents peculiarities of its own. The manus is incapable of supination in the usual way, but it reaches a position half-way between pronation and supination in the opposite direction; that is, by the rotation of the distal end

of the radius downwards instead of upwards. This movement may be called *antisupination*. In it the palm is presented outwards, and, when the humerus is flexed backwards, backwards also. This is its normal position when pushing the earth backwards from its burrow, and the muscles to accomplish this movement are enormously developed. These include the subscapularis, infra- and supraspinosus, and the triceps extensor. The act of antisupination of the manus is performed by the pronator muscles of the fore arm, and the effect of the rotation inwards of the distal end of the radius is to throw the proximal end outwards, so that it comes to be as external to the ulna at the cotylus, as in a quadrumane. The external condyle of the humerus is thus especially developed to receive it. In the act of anti-supination the head of the radius describes a movement in the transverse direction towards the external epicondyle, and the external condyle has been extended in that direction as a consequence of the continued thrust.

c. *The Femoro-tibial Articulation.* The existence of tibia and fibula of subequal size gave rise to two distal articular surfaces of the femur. The constant use of these in flexion and extension gave them the convexity which they possess in the Mammalia, a process already commenced in the Reptilia. The strong tendon of the rectus muscle passing over the anterior face of the extremity gave rise to the rotular groove. This became better defined and more important after the development in placental mammals of a sesamoid bone, or patella, in the tendon. The torsion of the femur on the arrest of the foot by the earth is, as with the humerus, from within forwards and outwards. To this cause, plus the impact, we may assign the production of the crest of the tibia in the same direction. The reason why, in the Reptilia, the fibula diminished in size, and the head of the tibia so expanded as to support the greater part of the external condyle of the femur, I am not at present able to suggest.

d. *The hinge between the first and second series of tarsal bones in the Artiodactyla* may be accounted for by reference to the habits which are supposed to have caused the cloven-footed character. Observation on an animal of this order walking in mud, shows that there is a great strain anteroposteriorly transverse to the long axis of the foot, which would readily cause a gradual loosening of an articulation like that connecting the two



series of tarsals in the extinct Amblypoda (Fig. 8). Any one who has examined this part of *Coryphodon* will see that a little additional mobility at this point would soon resemble the second tarsal joint of the Hippopotami, etc. In the case of animals which progress on hard ground, no such cross-strain would be experienced, and the effect

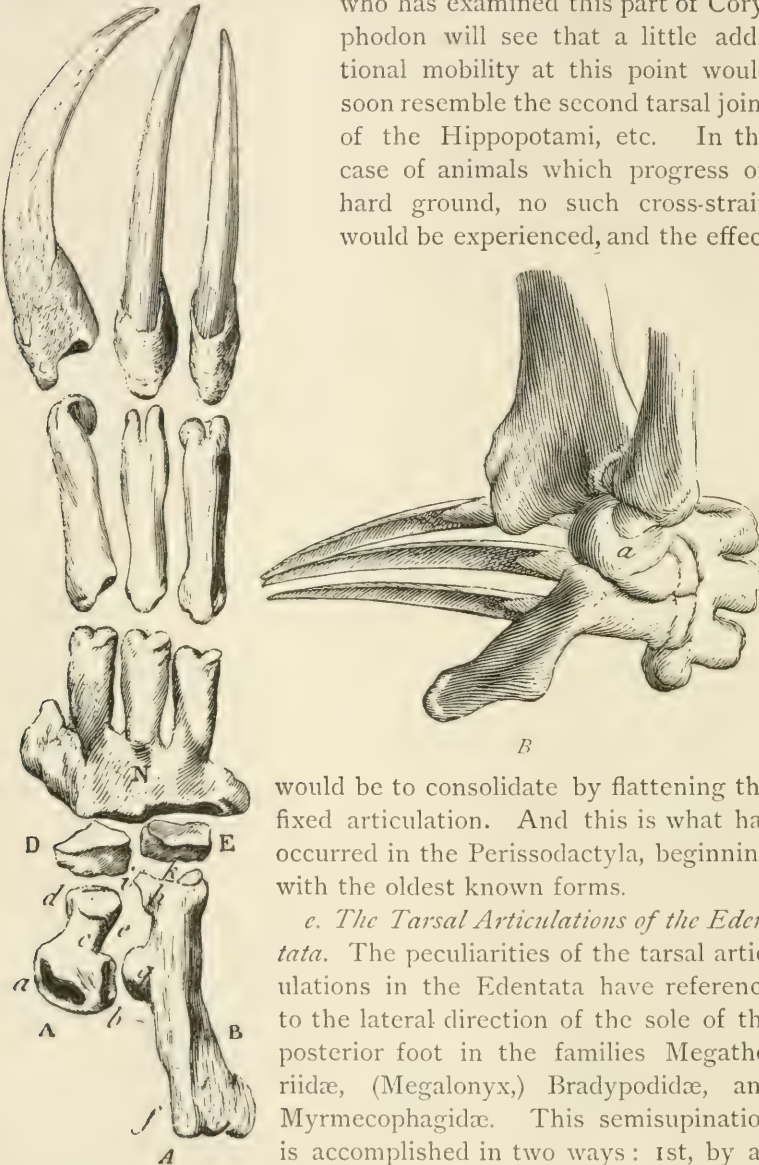


Figure 25.—A, *Bradypus tridactylus* L., posterior foot, from behind, nat. size: from Cuvier. B, *Cholopus didactylus* L., tarsus and end of leg, from behind, natural size: from Cuvier, Oss. Foss. a, Astragalus with peg and socket articulation of fibula.

would be to consolidate by flattening the fixed articulation. And this is what has occurred in the Perissodactyla, beginning with the oldest known forms.

c. *The Tarsal Articulations of the Edentata.* The peculiarities of the tarsal articulations in the Edentata have reference to the lateral direction of the sole of the posterior foot in the families Megatheriidae, (Megalonyx,) Bradypodidae, and Myrmecophagidae. This semisupination is accomplished in two ways: 1st, by an

oblique articulation between the tibia and astragalus; and second, by a rotation of the navicular on the rounded extremity of the astragalus. The first mode is seen in the *Megatheriidae*; the second in the *Megalonyx* and *Myrmecophaga*, and both combined in the sloths (*Bradypodidae*). The incurvature of the foot naturally resulted from the length and size of the claws, which rendered a truly plantigrade walk difficult or inconvenient, and thus compelled the animal to walk on the outside of its feet. In the modern sloths the lateral position of the tibio-tarsal articulation is an exact adaptation to the transverse direction assumed by the foot in hanging or walking while holding the body suspended beneath the branch on which the animal lives. The direction of the foot is at right angles to the longitudinal axis of the body, and across the branch to which it is suspended.

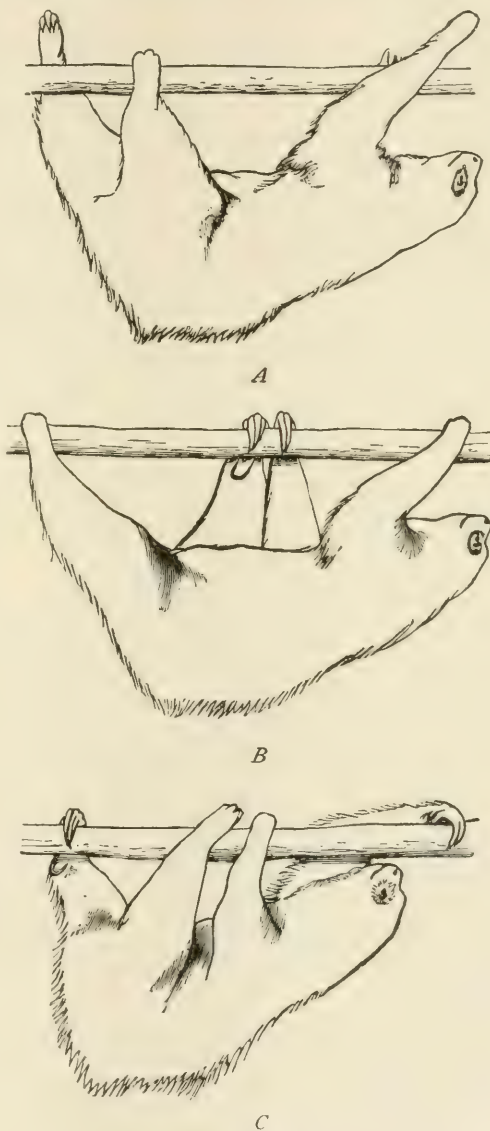


Figure 26. — *Cholapus hoffmanii*, in progression; three positions of the limbs; from Muybridge, *Animal Locomotion*.

The mechanical causes of these structures appear to be as follows. The strained incurvature of the foot has rotated the astragalus outwards on the tibia, so that the latter comes to articulate with its inner side, which has become continuous with the superior face by pressure. The stage intermediate between the normal tibio-astragalar articulation, and that of the sloth, is seen in *Megatherium* and *Mylodon*, where the inner part of the trochlea is reduced to a rudiment. In *Bradypus* it has disappeared. The pressure of the tibia has had the effect to throw the external face of the astragalus against the distal fibular articulation. In the sloths the articular ligaments connecting the fibular with the external face of the astragalus have been continuously strained, and the result has been the elongation of their more or less circular line of insertion, producing a prominent border which embraces the extremity of the fibula like a cup. And continual rotation has given the extremity of the fibula a conical form (Fig. 25 *B a*).

The movable articulation of the astragalus with the navicular bone is seen in *Megalonyx*, *Bradypus*, and to a less degree in *Myrmecophaga*. The foot rotates inwards on the long axis of the astragalus, which has a round head. This structure may be accounted for by the continued effort to perform the movement which it permits. It is to be noted that on this articulation the articular surface of the head of the astragalus presents a fossa, or a pit, into which a corresponding prejection of the navicular fits. The mechanical cause of this structure is to be accounted for by the ligamentous strain accompanying the vigorous use of the claws, which these *Edentata* exhibit in their habits. But why a rim border should be drawn from the astragalus rather than from the navicular, I am not able to explain. The calcaneum is excavated for the head of the astragalus, and the sustentaculum is convex; both arrangements permitting the rotation of the foot plus the calcaneum on the astragalus.

*f. The Tongue-and-Groove Joints.* These are the following:

I. Looking downwards.

1. The distal humeral in *Artiodactyla* and *Quadrupana*.
2. The distal radial.
3. The distal tibial.
- 4 and 5. The distal metapodial.

## II. Looking upwards.

6. The lateral proximal astragalar.
7. The proximal phalangeal.

I premise that the elbow joint comes under this head in the higher Diplarthra, but not being generally of this character, it has been already considered elsewhere (p. 179).

The trochlear keels which look downwards are much the most prominent and important. They are all projections from the ends of the respective elements. The up-looking are generally projections of the edges of bones. Such are the lateral crests of the astragalus, and of the phalanges of the Edentata. The tongues of the tongue-and-groove articulations exhibit various degrees of development in the different Mammalia. Those of different parts of the skeleton coincide in their condition in any one type of ambulatory Mammalia, and so may be all considered together. This fact suggests strongly that they are all due to a common cause. The proximal ridges of the phalanges are very weak except

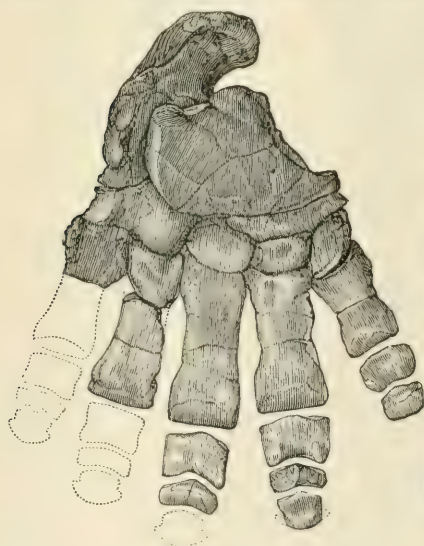


FIG. 27.

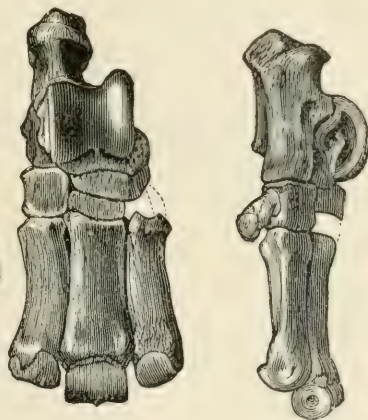


FIG. 28.

Figure 27.—Right posterior foot of a species of *Coryphodon* from New Mexico, one-half nat. size; from Report Expl. W. of 100th Mer., G. M. Wheeler, IV., Pl. LIX.

Figure 28.—Right posterior foot of *Aphelops megalodus* Cope, from Colorado, one-half nat. size; from Report U. S. Geol. Surv. Terrs., F. V. Hayden, IV., Pl. CXXX.



in certain Edentata; and crests on the extremity of the radius are adaptations to the carpal bones.

The tongues proper are all imperfect in the Rodentia and Carnivora (Figs. 5, 6) (except the Leporidae, which are especially characterized by their great speed). Among Ungulates they are very imperfect in the Proboscidea. The orders mentioned all have elastic pads on the under sides of their feet or toes. The same is true of the lowest types of both the Artiodactyla and Perissodactyla, the hippopotami and rhinoceroses. In the Ruminantia the trochleæ are well developed (Fig. 37) with one exception, and that is the distal metacarpal and metatarsal keels of the Camelidæ (Fig.

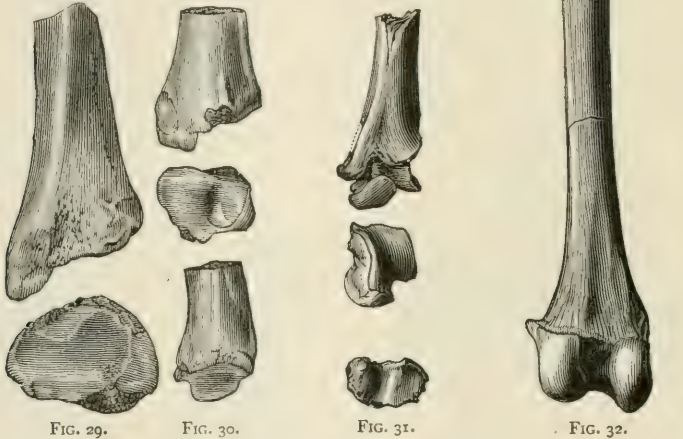


FIG. 29.

FIG. 30.

FIG. 31.

FIG. 32.

Figure 29. — Distal extremity of tibia of *Amblyctonus sinosus* Cope.

Figure 30. — Distal extremity of tibia of *Oxyæna morsitans* Cope. Both creodont flesheaters and two-thirds nat. size; from Report Expl. and Surv. W. of rooth Mer., G. M. Wheeler, IV., Pt. II.

Figure 31. — End of tibia and astragalus of *Archæolurus debilis*.

Figure 32. — Femur of *Nimravus gomphodus*. Both carnivores. One-third nat. size; Mus. Cope.

36). These animals confirm the probability of the completion of the keels being the effect of long-continued shocks, for they are the only Ruminants which have elastic pads on the inferior sides of their digits.

That these processes may be displacements due to shocks long continued is rendered probable by the structure of the

bones themselves. (1) They project in the direction of gravity. Constant jarring on the lower extremity of a hollow cylinder with soft (medullary) contents, and flexible end walls would tend to a decurvature of both inferior and superior adjacent end walls. If the side walls are wide and resistant, the projection will be median, and will be prolonged in the direction of the flexure of the joint. (2) They fit entering grooves of the proximal ends of corresponding bones. These will be the result of the same application of force and displacement, as the protrusion of the inferior, commencing with a concavity as in the astragalus (*Elephas*); becoming more concave (Plate II.), and becoming finally a groove. (3) When the dense edge of a bone, as in the case of the lateral walls of the astragalus, is presented upwards, a groove is produced in the down-looking bone; *e.g.* the lateral grooves of the distal end of the tibia. (4) When the inferior bones are the denser, the superior articular face yields; *e.g.* the distal end of the radius to the side walls and summits of the first row of carpals (Fig. 15). (5) All of these descending convexities have been converted into keels in the line of flexure by the long-continued torsion produced by the greater or less rotation of the bone with long axis. They have been thus pinched at all points of their length during flexures, but especially at their extremities.

To examine these cases in detail. In the ruminating animal's (ox, deer, camel, etc.) and in the horse, among other living species, the ankle joint is a very strong one, and yet admits of an extensive bending of the foot on the leg. It is a treble tongue-and-groove joint; that is, two keels of the first bone of the foot, the astragalus, fit into two grooves of the lower bone of the leg, the tibia, while between these grooves a keel of the tibia descends to fill a corresponding groove of the astragalus. Such a joint as this can be broken by force, but it cannot be dislocated. Now, in all bones the external walls are composed of dense material, while the centres are spongy and comparatively soft. The first bone of the foot (astragalus) is narrower, from side to side, than the tibia which rests upon it. Hence the edges of the dense side walls of the astragalus fall within the edges of the dense side walls of the tibia, and they appear to have pressed into the more yielding material that forms the end of the bone, and pushed it upward, thus allowing the side walls

of the tibia to embrace the side walls of the astragalus. Now, this is exactly what would happen if two pieces of similar dead material, similarly placed, should be subjected to a continual pounding in the direction of their length for a long period of time. And we cannot ascribe any other immediate origin to it in the living material; but the probability of such origin is more probable in such substance, because of the perpetual waste and repair which are going on, as illustrated by the power which we see in growth, in repairing damages, and in providing for new conditions in cases of accident. The inclusion of the astragalus in the tibia does not occur in the Reptiles, but appears first in the Mammalia, which descended from them.

The same active cause that produced the two grooves of the lower end of the leg produced the groove of the middle of the upper end of the astragalus. Here we have the yielding lower end of the tibia resting on the equally spongy material of the middle of the astragalus. There is here no question of the hard material cutting into soft, but simply the result of continuous concussion. The consequence of concussion would be to cause the yielding faces of the bones to bend downward in the direction of gravity. If they were flat at first they would begin to hollow downward, and a tongue above and a groove below would be the result. And that is exactly what has happened. Without exception, every line of Mammalia commenced with types with an astragalus which is flat in the traverse direction, or without median groove. From early tertiary times to the present day, we can trace the gradual development of this groove in all the lines which have acquired it. The upper surface becomes first a little concave; the concavity gradually becomes deeper, and finally forms a well-marked groove.

The history of the wrist-joint is similar. The surface of the fore-arm bones which joins the fore foot is in the early tertiary Mammalia uniformly concave. In the ruminating mammals it is divided into three fossæ, which are separated by sharp keels. These fossæ correspond with the three bones which form the first row of the carpus or palm. The keels correspond to the sutures between them. The process has been evidently similar to that which has been described above as producing the side grooves in the end of the tibia. The dense walls of the sides of the three bones impinging endwise on the broad yielding sur-

face of the fore arm (radius) have gradually, under the influence of countless blows, impressed themselves into the latter. On the contrary, the surface above the weaker lines between the bones not having been subject to the impact of the blows, and influenced by inertia and gravity, remains to fill the grooves, and to form the keels which we observe.

We now consider the development of the keels and grooves which appear at the articulation of the metapodials

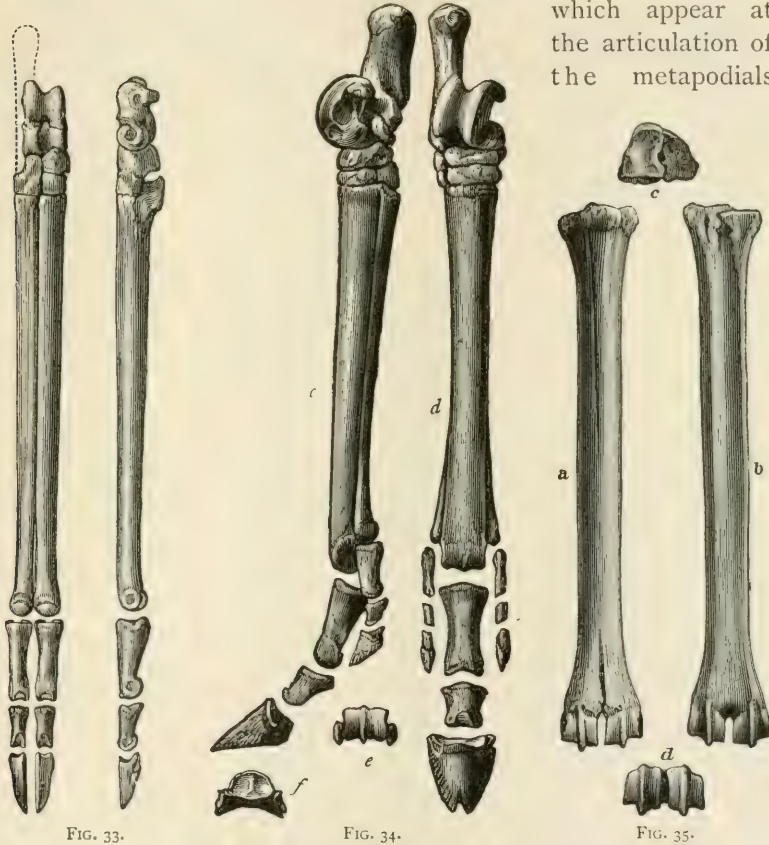


FIG. 33.

FIG. 34.

FIG. 35.

Figure 33. — Hind foot of primitive cameloid (*Pöebrotherium labiatum*), showing grooved astragalus and first toe-bones, without keel, in front at lower end; from Colorado.

Figure 34. — Hind foot of three-toed horse (*Protohippus sejunctus*), from Colorado, showing grooved astragalus, and trace of keel on front of lower end of first bone of middle toe.

Figure 35. — United first bones of two middle toes of deer-antelope (*Cosoryx furcatus*), showing extension of keel on front of lower end; from Miocene of Nebraska.



with the bones of the second set (phalanges). These keels first appear on the posterior side of the end of the first set of bones, projecting from between two tendons. These tendons, in most mammals, contain two small bones, one on each side, which act like the knee-pan and resemble it in miniature, the sesamoid bones. These tendons and bones exercise a constant pressure on each side of middle line, when the animal is running or walking,

when extension of the phalanges is most pronounced; and this pressure, together with the concussion with the ground and the torsion of the limb, appears to have permitted the protrusion of the middle line in the form of a keel, while the lateral parts have

been supported and even compressed. The reptilian ancestors of the mammals do not possess these keels.

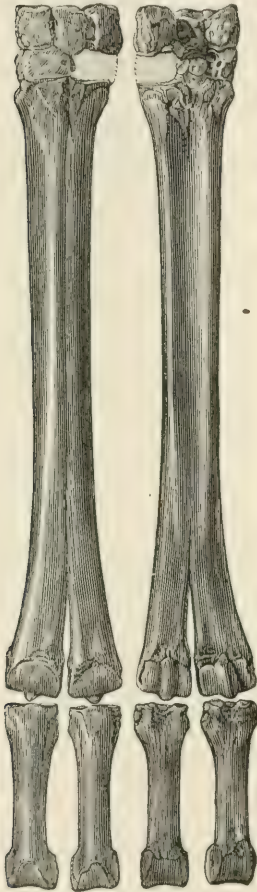


FIG. 36.

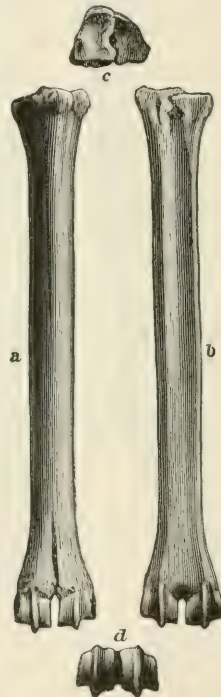


FIG. 37.



FIG. 38.

Figure 36. — Part of anterior foot of *Procamelus occidentalis*, from New Mexico; from Report of Capt. G. M. Wheeler, Vol. IV., Pt. II.

Figure 37. — Metacarpals of *Cosoryx furcatus*, from Nebraska, two-thirds nat. size: *a*, anterior face; *b*, posterior; *c*, proximal end; *d*, distal end.

Figure 38. — Left fore foot with part of radius of *Poebrotherium wilsoni* Leidy, from Colorado, three-fifths nat. size; from Hayden's Report, III., (unpublished).

Now, the lines of mammalian descent displayed by paleontology are characterized, among other things, in most instances, by the gradual elevation of the heel above the ground, so that the animal comes to walk on its toes. It is evident that in this case the concussion of running is applied more directly on the ends of the bones of the foot, than is the case where the foot is horizontal. As a consequence, we find the keel is developed farther forward in such animals. But in many of these, as the Carnivora, the hippopotamus, and the camels, there is developed under the toes a soft cushion, which greatly reduces this concussion. In these species the keel makes no further progress. In other lines, as those of the horse, the pig, and of the ruminants, the ends of the toes are applied to the ground, and are covered with larger hoofs, which surround the toe, and the cushion is nearly or quite dispensed with. These animals are especially distinguished by the fact that their metapodial keels extend entirely round the end of the bone, dividing the front, as well as the end and back, into two parts. This structure would seem to be a result of the greater force of the impact resulting from use of the legs, experienced by the end and front of the bone, which receives the blows. In proportion to the degree of digitigradism is the strain on the tendons at plantation and recover. In running, in the digitigrade Ungulata, the toe is antiflexed so as to bend at right angles anterior to the metapodial bone, just before leaving the ground (recover). It is the strain and torsion at this moment that has produced the tongue to the front of the metapodial. It is also evident that the elevation of the heel offers the condition for torsion strain on the leg immediately following contact with the ground. This agency has been especially considered under the head of the fixed articulations.

The distal phalangeal articulations are usually simply concave, receiving a median angle from the phalanges distad. This median concavity is probably the result of the impact on the ground, of a surface narrower than the excavated extremity, viz. : of the apex of the unguis. This impact exerts the greatest displacement along the median line or axis of the digit. Apart from this, however, a determining cause of the simplicity of the phalangeal groove is found in the undivided flexor tendon and the single sesamoid bone, both of which exercise considerable pressure on the median line, when the weight of the body is thrown

on the extremities of the digits, and they are thus excessively extended.

Especial peculiarity of phalangeal articulation is to be seen in the Edentata. This consists of the deepening

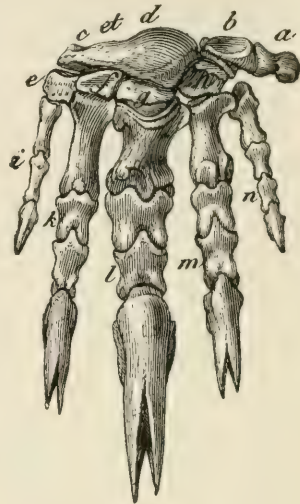


FIG. 39.

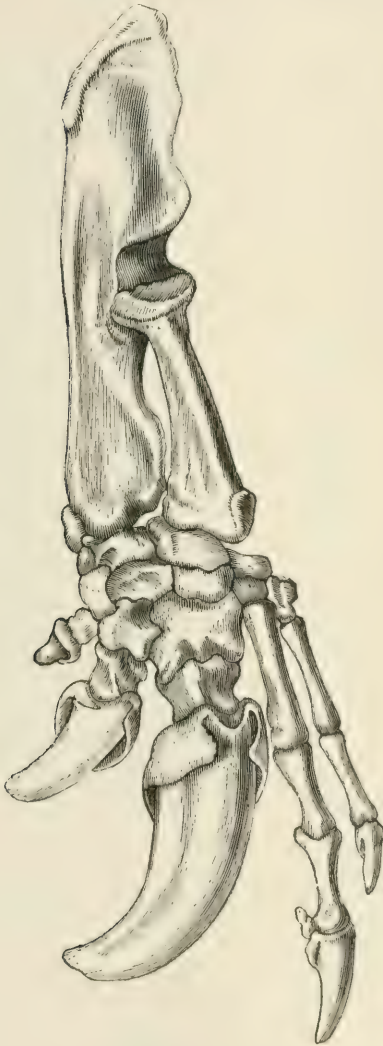


FIG. 40.



FIG. 41.

Figure 39. — *Manis indica*; manus natural size; from Cuvier, Oss. Fos.

Figure 40. — *Priodontes maximus* Kerr, fore arm and manus; from Cuvier.

Figure 41. — *Priodontes maximus* Kerr, pes; original.

of the distal groove so as to render the articulations, tongue and groove, like the tibio-astragalar articulation of *Diplarthra*. This structure gives great strength, and an increased protection against dislocation. It exists in both feet of the *Manidæ* and *Myrmecophagidæ*, and in the anterior digits of the *Dasypodidæ* which have especially developed ungues (Figs. 37-39). The fact that the ungues differ in this respect in the armadillos, *e.g.* *Priodontes maximus*, gives us an excellent opportunity for investigating the origin of the structure. The first and second digits of the fore foot present perfectly simple phalangeal articulations. The ungues are slender, and from their position take no part in excavation of the earth. The ungues of the third and fourth digits are enormously developed, and are chiefly used in excavation. The phalanges display the tongue-and-groove joints. The ungues of the posterior foot resemble hoofs in form and function, and the phalangeal articulations are flat and simple, greatly resembling those of primitive ungulate Mammalia, except that they have no trace of keel posteriorly. The close relation of function to the structure is here obvious. The deep tongue-and-groove articulation is a consequence of the excessive use of the digits which exhibit it, in the excavation of the earth. The mechanical cause of the structure must be in the main similar to that which gave origin to the tibio-astragalar articulation of the *Diplarthra*, but it has acted in the reversed direction; that is, the median groove looks downwards and the keel looks upwards. This difference is to be traced to the different conditions under which the respective processes commenced. In the case of the tibia, the extremity was primarily convex downwards, owing to the coöperation of impact with gravity. The distal extremity of the phalange was originally concave, owing to the pressure of a median tendon and sesamoid bone. In each case the continued application of the strain would tend to exaggerate the original condition. After a certain extent of arc of the phalangeal articulation has been reached, the sesamoid bone has little effect, and the continued growth of the keels must be due to continued impacts combined with torsions of the digits; the impacts affecting most energetically the middle line. The torsion movement would have the effect to compress the keels exactly in the line or arc of flexion and extension, by alternate



pressure on their sides, as in the case of the distal keels of the metapodials.

The relative character of the phalanges of the different feet seen in *Priodontes maximus* finds a parallel in the Glyptodontidæ. Here the tongue-and-groove articulations are strong on the anterior feet, and altogether wanting on the posterior.<sup>1</sup> The ungues on the former are half-claws, and are evidently usable for digging, while those of the pes are hoofs, usable only for support or pressure. The relation of cause and effect is as obvious here as in the case of the *Priodontes*.

Finally, the mechanical effect of the torsion strain on the convexity of a condyle in converting it into a keel, may be noticed in greater detail. The result mentioned appears in the distal condyles of the humerus in the Diplarthra, at the distal extremities of the metapodials in many Mammalia, and in the phalangeal articulations of fossorial types. The effect of a twisting motion of a convex or a concave surface when in close apposition, is to cause pressure and friction on each side of a central dead-point, which is at the centre of the curve. If these surfaces change their relative positions in one plane through flexion and extension, a line of dead points at the apex of the convexity is free from the pressure and friction which are developed on each side of it. The greater the arc of movement in this plane, the more extensive will be this dead line. The greatest movement in arc results where the one surface has a shorter arc than the other. The concave surface has the smaller arc in the three positions named, and has also the greatest movement in arc, as it is in each case the distal element.

The internal and external sides of the distal metapodial condyles are not similar; a character very distinct in the Artiodactyla (Fig. 42). This is simply due to the unequal pressure exerted on the two extremities of the condyle by the phalanges, owing to the divergent direction of the digits when serving as a support. In the distal end of the humerus the same effect is seen, the external part of the condyle nearly resembling the corresponding part of the metapodial bones. This is traceable to the same cause, viz.: the divergent position assumed by the fore arm on the humerus, when the weight is supported on one

<sup>1</sup> See Burmeister, *Archiv. für Anatomie u. Physiologie*, 1865, p. 317, Pl. VIII.

fore leg only. This brings the line of pressure through the external part of both the head of the radius and the humeral condyle (Fig. 23).

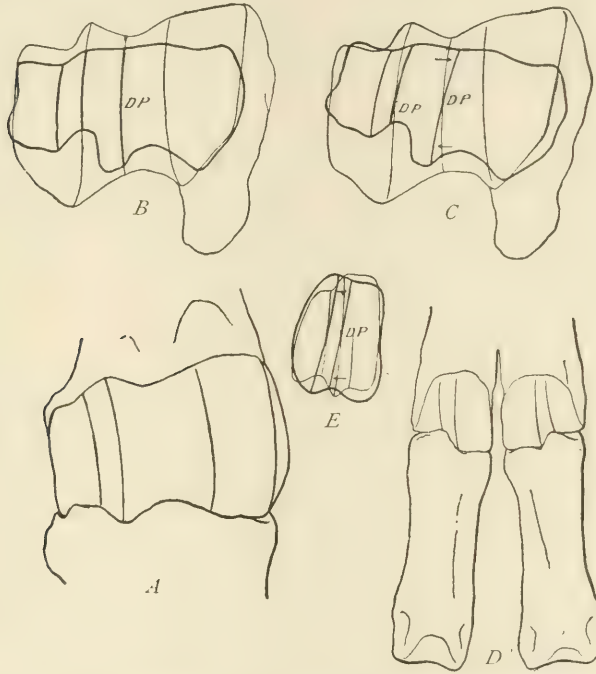


Figure 42.—*Cervus elaphus*; A, B, C, humero-radial articulation; A and C, with the radius in position; B, with radius twisted; D, E, metatarsophalangeal articulation; D, front; E, distal views.

In conclusion, the tongue-and-groove articulations of the mammalian limbs and their origin may be summarized.

I. *Intertrochlear crest of humerus of Anthropomorpha.* Originated from plastic adaptation to space between head of ulna and coronoid process of ulna.

II. *Trochlear crest of humerus of Diplarthra.* Originated from impacts, torsions, and exterior divergence of fore arm on humerus.

III. *Intercarpal crests of radius of Artiodactyla*; from plastic adaptation to intercarpal grooves.

IV. *Metapodial keels*; from impact, torsion, and pressure of two posterior ligaments and sesamoid bones, and if unsymmetrical, as in Artiodactyla, modified by divergence of digits.

V. *Proximal phalangeal keels*, from impacts derived from apex of unguis, torsion, and pressure of single median tendon and sesamoid bone on distal end of proximal phalanges.

VI. *Astragalo-tibial keel*; impact and torsion aided by gravity.

VII. *Tibio-astragalus keels*; from pressure of dense edges of astragalus on spongy end of tibia, with impacts and torsion.

## II. THE AXIS OF THE SKELETON.

The discussion of this part of the skeleton falls naturally into the departments of the skull and of the vertebral column.

### I. THE SKULL.

#### a. *The Sense Organs.*

The modifications in the form of the skull are generally directly related to the muscular strains to which it is subjected. The size of the brain cavity is directly as the development of the brain, especially of the hemispheres. The size of its sense capsules is directly as the activity of the sense which they subserve. With diminution of the sense of sight the definition of the osseous orbits grows less and disappears, as in the mole and other subterranean species. Nocturnal species which are constantly stimulated by diminished, but not extinguished light, have acquired large eyes, which occupy large orbits. Species in which the sense of smell is atrophied have very small nasal chambers, as the Cetacea.

As regards the modification in the proportions of the skull in adaptation to the brain and organs of special sense, they cannot be said to be due to direct mechanical interference of the latter, in impressing the former. The changes in proportions are here effected during embryonic life by the change in the distribution of building material. The brain and organs of sense are outlined in the embryo before the skull has attained any rigidity, and the latter may be truly said to be moulded on the former. We have here an illustration of the effect of use which is not mechanical, since the softer tissue of the brain and sense organs cannot coerce the harder tissue of the skeleton. It shows how that use, whether it effect mechanical changes in the hard tissues or not, produces a distinct

change in the distribution and determination of growth-energy in the embryo. This sustains the dynamic theory of heredity which I proposed in 1871, and which was subsequently termed perigenesis by Haeckel. Such a hypothesis is equally necessary to explain the transmission of characters, which are more or less developed in the adult by the mechanical energy of impacts and strains.

*β. The Muscular Insertions.*

As regards muscular insertions, the best marked are those for the muscles supporting the head on the vertebral column, and for moving the lower jaw in mastication. Strength of the former has developed the strong occipital crest of the inion. Size of the temporal muscle determines the expanse of the zygomatica, and the presence or absence of a sagittal crest. Forms which move the lower jaw transversely have the temporal muscles inversely as the extent of the lateral excursions of the jaw. Hence these muscles have a diminished size in such forms as the ruminants, and are widely separated. On the other hand, the pterygoid muscles and their osseous insertions are enlarged. This is still more the case with forms which have an anteroposterior movement of the lower jaw, as the Rodentia and Proboscidea, where the pterygoid fossa is very large.

The position of the dental series with reference to the skull in general has reference to the energy of the action of the temporal and masseter muscles. In primitive Mammalia a considerable part of the molar series is below and posterior to the position of the orbit, and the series has been prolonged posteriorly in forms which possess the proal or palinal mastication, as Rodentia and Proboscidea. In forms with ectal or ental mastication, on the other hand, the molar series has gradually moved forwards so as to be entirely anterior to the vertical line of the orbit, as in the horse and the Bovidae. The camel retains the primitive relation in this respect.<sup>1</sup> This apparent anomaly may be explained by the fact that the camel retains large and powerful canine teeth, which he uses as weapons of offence and defence, so that his temporal muscles retain the large development of the early forms. This is further indicated by the

<sup>1</sup> See Kowalevsky *Monographie d. Anthracotherium*, 1873, Pl. IX.



presence of a sagittal crest, the only instance of its presence in existing selenodont Artiodactyla. The forms of bunodont Artiodactyles with the orthal mastication (*Elotherium* and *Dicotyles*) have the molar series posterior; those with lateral movement of the lower jaw (*Suidæ*, *Phacochoeridæ*) have them rather more anterior. In man, also, the dental series retains its primitive posterior position, but for very different reasons. The large development of the cerebral hemispheres has caused the retention of the primitive foetal flexure of the cranium, and the anterior part of the dental arcs has even retreated from the position it occupies in the apes. The non-retreat of the inferior part of the mandibular symphysis has caused the appearance of the chin, a feature so characteristic of man.

The use of the canine teeth as organs of prehension in the Carnivora is directly followed by the abbreviation of the muzzle, as in the bull-dog, the hyænas, cats, etc.

The mechanical cause of these various positions may be interpreted as follows: In vertical action of the lower jaw, the use is severe directly as we approach the power; *i.e.* the point of insertion of the temporal and masseter muscles. The posterior teeth will then acquire the greatest development, and will continue to be erupted at the region of the greatest nutritive activity, *i.e.* posteriorly. In the case of the Rodentia there is another mechanical influence, *viz.*: the posterior horizontal pressure exerted by the inferior series on the superior. Why the Proboscidea should retain the posterior position of the superior molar teeth, while the pressure of the inferior molars is in the opposite direction, *i.e.* from behind forwards, is not readily explicable at present. But it is evident that, owing to the extraordinarily vigorous use to which the superior incisors are subjected, as in the case of the canines of the Carnivora, that natural selection would preserve the short-muzzled forms in competition with long-muzzled ones.

The modification of the skull which the Cetacea and Sirenia have undergone with the lapse of geologic time, is well known. In the earliest known representatives of the order Cetacea, the Zeuglodontidæ, the external nostrils occupy a point on the superior face of the muzzle approximately half way between the lines of the premaxillary and anterior frontal borders, and the nasal bones are elongate. In the Balænidæ the frontal is

crowded back to the parietal, and the latter forms but a narrow band in front of the occipital, while the nasals form but a short roof over the nostrils, which are now above the eyes. In the Delphinidæ the nostrils have an even more posterior position, and the nasal bones take part in the extreme shortening already seen in the frontals and parietals. The convenience of this location of the nostrils is evident. It relieves the animal of the necessity of raising the muzzle from the surface of the water in taking an inspiration; a convenience which becomes a necessity in the two families last named, when the cervical region has become so short as to render such a movement impossible.

The mechanical energy which has caused this posterior retreat of the nostrils appears to me to have been the constant pressure of a column of water from below, *i.e.* from the mouth. This constant discharge through the nostrils appears to me competent to force the oblique superior wall of the nasal canal to become a vertical one, and to shorten the nasal bones from before backwards, until they cease to obstruct the outgoing current.

#### *γ. The Horns.*

Horns are developed in Mammalia and other Vertebrata on similar parts of the skull, principally on the posterior lateral angles, as in various Batrachia, Reptilia, and Mammalia, and on the nose, as in a few Mammalia and several reptiles, recent and extinct. These parts are the ones which are especially brought into contact with resisting bodies; the nose in pushing a path or way for the head and body; the lateral occipital region in defence and assault, when the sensitive nose and eyes are protected by being held near the ground. In the latter position the postero-lateral angles, when present, receive more frequent collision with, and vigorous stimulation from, a body attacked or resisted, and in accordance with the observed results of irritation on dermal and osseous tissues, additional matter has been deposited. In Lacertilia and Batrachia Salientia there are distinct postero-external cranial angles; in Batrachia Urodela such angles are less prominent. In Unguiculate Mammalia and in all others with a sagittal crest there are no such angles; hence this type of skull has never developed posterior horns. The rhinoceros has developed the dermal nasal horn, and the Elas-

motherium, a median osseous horn, since postero-lateral angles of the skull are wanting. In the Dinocerata and the Artiodactyla, where the temporal crests are lateral, leaving a wide frontoparietal plane with posterior lateral angles, horns are developed. In members of both groups horns have been developed over the orbits also (Fig. 43), and in the Dinocerata on the extremities of the nasal bones as well. These growths are all on parts which are subject to especial irritation by contact with other bodies, animate and inanimate.

Among Artiodactyla, the deer (*Cervidæ*) are especially distinguished by the periodical shedding of all but the bases of their horns. Extinct forms found in the Upper Miocene of the United States and France (the Loup Fork series) furnish the explanation of the origin of this remarkable peculiarity. In the genus *Cosoryx* we find that the horns may or may not possess a burr near the base of the beam, like that of the deer; the same species being indifferently with it or without it. This observation has been made on three species, — the *C. necatus*, *C. furcatus*, and *C. ramosus*. The following explanation of these facts has been proposed by myself.<sup>1</sup> "From the facts of the case the following inference may be derived, premising that it is very probable that a genus allied to the present one has given origin to the family of the deer. It is obvious that the horns of (*Dicrocerus*) *Cosoryx* did not possess a horny sheath as in the *Bovidæ*, from the fact of their being branched. As the sheath grows by addition at the base, the presence of branches which necessarily obstruct its forward movement, would be fatal to the process. There is much to be said in favor of the view that the horns were covered with an integument, probably furred, as in the giraffe and young stage in the deer. Thus there are grooves in the surface of the beam for superficial blood-vessels, which must have been protected by skin (I do not observe these grooves on the beam of *C. teres*). The retention of the broken extremity of an antler, so as to be reunited, as described (Fig. 43, 3), could not have been accomplished without an integument. The presence of the burrs cannot be accounted for on any other supposition, as there are no foramina to give exit to nutrient vessels at the point where they exist;

<sup>1</sup> *U. S. G. G. Survey west of the 100th Mer.*, G. M. Wheeler: iv., *Paleontology*, 1877, p. 348.

the irregularity of those positions also forbids the latter idea, and adds to the probability that the arteries which furnished the deposit of phosphate of lime were contained in a superficial dermal coating. The supposition is also strengthened by the fact that the only existing Ruminants (the giraffes) with permanent horns without horny sheaths have them covered with hairy skin.

"It appears that in the antlers of *Cosoryx* the deposit of a burr was immediately associated with the death of the portion of the horn beyond it, so that it disintegrated and disappeared.

This was not the case with the beam in the specimens observed. Nevertheless it is probable that the death of the horn would be associated with the deposit of the burr in this case also, were the conditions the same. What those conditions were we can only surmise. It was very probably the death of the integument which invested and nourished the horn that produced that result; and this would more readily occur in the exposed antlers than in the more protected basal portion of the beam. It is very probable that this result would follow blows and laceration of the surface received during com-

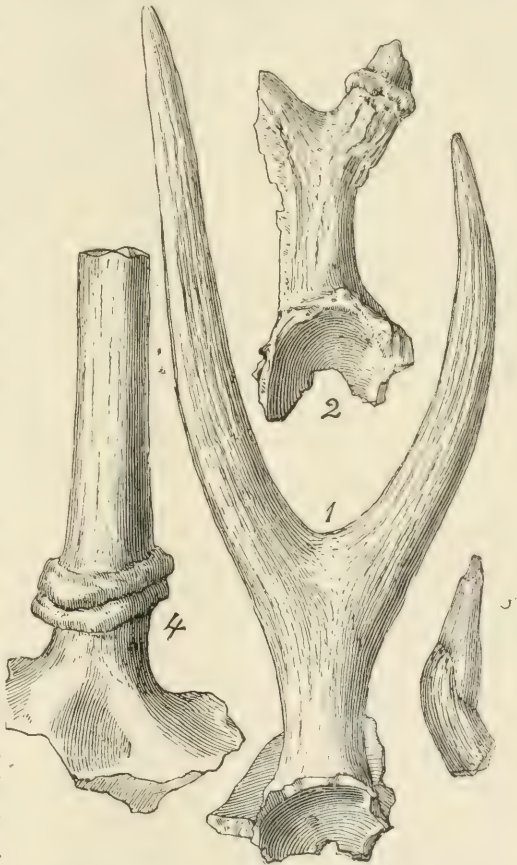


Figure 43. — 1, 2, *Cosoryx necatus* Leidy; 1, without, 2, with, burr on antler; 3, 4, *Cosoryx ramosus* Cope; 3, antler broken and reunited; 4, beam with burr; two-thirds nat. size; original; from Report U. S. G. G. Expl. 100th Mer., G. M. Wheeler.



bat, or accidental contact with hard substances. The integument would be stripped up to near the junction of the antlers with each other, or of the beam with the cranium, and the arteries would be constricted or closed at those points. It is near these junctions that all of the burrs are found. But as such lesion would be necessarily less complete at the point where the horn has greatest circumference, so the entire death of the horn might be less usual than that of the branches. Should such lesions have occurred for a long period at the breeding season, nature's efforts to repair by redeposit of bony tissue might as readily become periodical as the increase in size and activity of the reproductive organs and other growths which characterize the breeding season in many animals. The subsequent death of the horn would be at some time followed by its shedding by the ordinary process of sloughing."

Cosoryx is not the true ancestor of the Cervidæ, as its teeth have already attained the prismatic type of the higher Bovidæ. But Blastomeryx is most probably the ancestor of the deer. The remains of this genus occur with those of Cosoryx, but the burr has not yet been observed on its horns.

## 2. THE VERTEBRAL CENTRA.

### *a. The Articular Faces.*

The mutual articulations of the vertebral column are these of the centra and of the zygapophyses. Many important modifications in these articulations are to be seen in Vertebrata, the Reptilia presenting the greatest variety, excepting in the zygapophyses, which are tolerably uniform in that class. In the Mammalia modifications of the central articulations are not more striking than are those of the zygapophyses.

The forms of central articulation are four; viz.: the amphicœlous, the ball-and-socket, the plane, and the saddle-shaped. The first type is only seen in a very imperfect degree in Mammalia and in but very few vertebræ, where it is indeed but a modification of the plane. The ball-and-socket is chiefly found in the neck of long-necked Mammalia, as the higher Diplarthra, and to a less degree in their lumbar regions, while the dorsal vertebræ present an approach to the same type in the same groups. The saddle-shaped centrum is only found in

Mammalia in the necks of certain genera of monkeys. The majority of Mammalia present the plane articulation of all the vertebral centra.

In Mammalia in which movement of the vertebræ on each other has become impossible, the centra coössify. Such is their condition in the extinct Edentata of the family Glyptodontidæ, where the carapace is, as in the tortoises, inflexible, and which therefore limits the possibility of motion of the vertebral column. Another illustration is seen in the necks of the Balænid Cetacea, and to some degree in the Delphinidæ and Physteridæ. The lack of present mobility of this part of the column is due to its extreme abbreviation, a character which has been gradually developing during Cænozoic time; since the earliest Cetacea had considerably longer necks than the later ones, and had their vertebral centra distinct. I cannot account positively for this shortening of the neck, but will make a suggestion which may prove to be sufficient. It appears to me probable that the shortening was the result of disuse. This disuse would arise from gradually increasing powers of locomotion through the water, a progress which, judging from the character of the limbs of the Zeuglodon, was evidently made after the time of the Eocene. The increase of speed would enable the animal to overtake and capture its prey, without the necessity of using a long prehensile neck in seizing it in the pursuit.

The ball-and-socket articulation of the vertebræ is well known to be the predominant condition in the Reptilia, and the fact that it is necessarily associated with the flexibility of the column is equally well understood. This flexibility is directly as the weakness of the limbs, for in the large terrestrial Reptilia of the order Dinosauria, the vertebral articulations of the dorsal region, at least, are plane. That it is chiefly confined to, and best developed in, the most flexible regions of the column of the Mammalia also shows this necessary connection. There can be no doubt but that the ball-and-socket vertebral articulation has been produced by constant flexures of the column in all directions, as has been suggested by Marsh.

The saddle-shaped articulation permits great lateral and vertical flexure, but none in any other direction. Longitudinal torsion is impossible. It is a more secure articulation than the

ball-and-socket, and admits at the same time of more abrupt flexure than the latter. It may have arisen in birds from a combination of two causes. One of these is the much greater

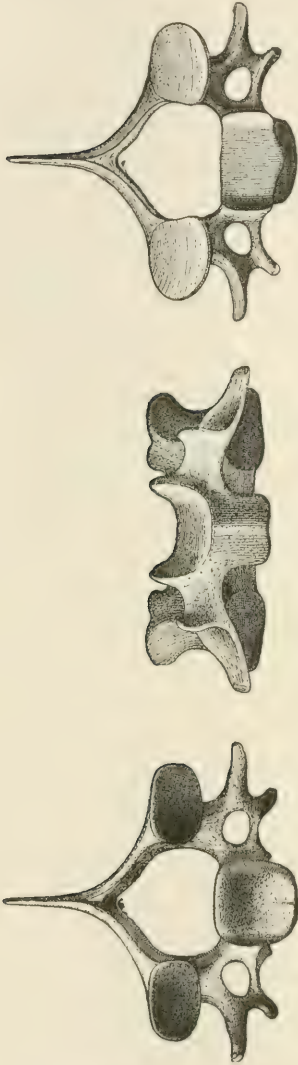


Figure 44. — Cervical vertebrae of *Cynocephalus*, showing saddle-shaped centra.

frequency of the vertical and lateral flexures of the cervical region than any others. These are seen in the vertical flexure of the neck when in ordinary repose; and the horizontal flexure when the head is placed under the wing during sleep. A greater tension of the intervertebral ligaments than is found in cold-blooded or even other warm-blooded invertebrates, would encourage an especial activity of nutrition in the regions of greatest stress, when the column was flexed in the two habitual directions, and thus the edges of the primitive cups be drawn out in the directions in which we find them. This would seem to be a reasonable explanation of the origin of this type in birds, and it may apply to the cervical region of the monkeys, which display it. They frequently sit with the head resting on the shoulders and the neck bent in an anteroposterior sigmoid. Whether they lean the head to one side or on the shoulder, during sleep, I have not had the opportunity to observe.

The plane vertebra, like the other types, was derived from the biconcave or amphicœlous, by ossification of the intervertebral cartilage. This cartilage is divided, each half forming the epiphysis of a centrum (Hoffman), and in the Mammalia without forming a ball-and-socket

joint. This was clearly for the reason that movements of the vertebral column were not necessary for locomotion, which was performed by the aid of stout limbs, on land.

*β. The Relative Lengths of the Vertebrae.*

The extreme abbreviation of the cervical vertebrae in the Cetacea has been already referred to, and a cause suggested. This is the disuse naturally following increased power of turning the body about in the medium in which they live. As a matter of fact the inverse relation between the two functions may be observed in many marine Vertebrata. Such are fishes in general, marine turtles, and Ichthyosauri. A few fishes (Dercetidae) and the Plesiosauri had long necks, but these animals may be supposed to have used their necks in exploring holes in reefs or the shores and bottom of the ocean.

Great elongation of the tail and neck is found in certain types; the former especially in some Edentata (Manis) and Rodentia, and the latter in Artiodactyla. Length of tail may be regarded as an inheritance from, or reversion to, Reptilian ancestors; but length of neck is a direct adaptation to the habits of the animal, and is always correlated with length of the fore legs. In animals which take their food from the ground it is not difficult to see in it a result of strains in the long direction, aided by gravity, as in the Hyænas and Artiodactyla; but in those which browse like the giraffe, the mechanical conditions are different. I cannot demonstrate the correctness of the view of Lamarck that the enormously long neck of the giraffe was produced by continuous stretching upwards. Muscular contraction can only result in the straightening of the neck and limbs, but not in the application of any extensor energy. For the present we may suppose that the mere effort of straightening the limbs and neck long continued would be equivalent to use and would determine nutrition to the parts. With the straightening would occur numerous lateral strains, which would conduce to the same result.

In the Hyænas the case is clear. The fore legs and neck are subjected to especial strain in their mode of feeding. After Canidae and Felidae have deprived a carcass of much of its flesh, the Hyænas devour the skeleton and ligaments. Their



task requires much more force for its execution both in the fore legs and feet in holding the bones to the earth, and in the neck in dragging them asunder; while the task of comminuting them is performed by the large sectorial molar teeth, the most powerful and massive in the entire order of Carnivora.

### 3. THE VERTEBRAL ARCHES.

The mechanical cause of the origin of neural spines may be traced to the strains upon the vertebral axis caused by a primary dorsal fold or fin; and in later and terrestrial types, to the strains imposed by the presence of the dorsal muscles. The existence of diapophyses may be perhaps assigned to the strains from the two primitive lateral folds from which the pectoral and ventral fins were evolved. The zygapophyses occupy the space on the vertebra, between these two fulcral points, and constitute an important element in the interlocking of the vertebræ. Of an efficient mechanical cause for their origin we are ignorant, and the search for it would more appropriately belong to the investigation of the lower vertebrata than to the present paper. I only recall here that the crests of the zygapophyses are the seat of the insertions of a part of the *multifidus spinæ* muscle, and receive its strains.

Mammalia present important peculiarities of the zygapophyses. That these are well-marked may be derived from the accompanying plates III.-VI. The primitive form of simple flat surfaces prevails in the lower orders, offering only differences in their greater or less obliquity. In Manis, the Creodonta, and the Ungulata, this obliquity assumes an interlocking character. The prezygapophysis becomes concave in transverse vertical section, forming an anteroposterior canal, while the postzygapophysis becomes a partial anteroposterior cylinder, which fits within the former. In the Artiodactyla the structure is further modified in various genera. In Sus and Capra as extreme examples, the postzygapophysis becomes sigmoid in transverse section, its external surface displaying a longitudinal cylinder below, continuous with a groove above, the whole surmounted by the overhanging edge of the roof of a process, or episphe.

Since these structures appear only in the lumbar region, where motion is possible owing to the absence of rib connections, and

where the greatest weight of the body is supported, we are at once directed to strains as their cause. We cannot trace them to vertical strains, since the semi-cylinders and their embracing channels are perfectly horizontal, and not bent so as to permit vertical flexure of the column. They are not due to lateral curvature of the column, for then each cylinder would be convex externally in the longitudinal direction, or perhaps much abbreviated anteroposteriorly. They appear to have been caused rather by longitudinal torsion of the column.

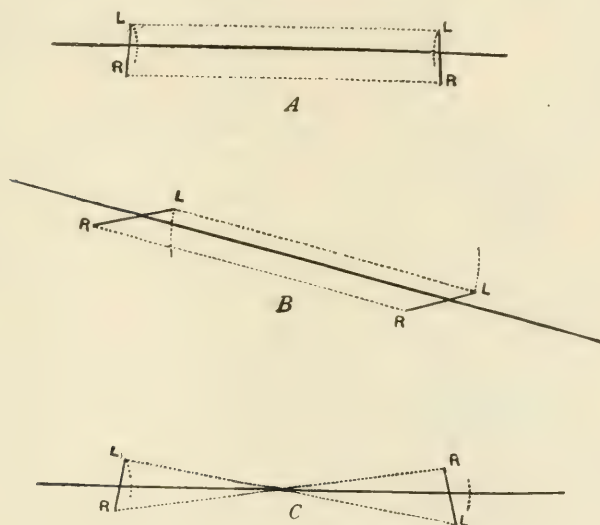


Figure 45. — Diagrams representing the movements of the vertebral column in *A*, the pace; *B*, the run; and *C*, the trot or walk.

The mechanical cause of this torsion is as follows. Viewed from the standpoint of their mechanical effects on the skeleton,<sup>1</sup> the gaits of animals may be referred to three types. The first is that in which the both feet of a pair strike the earth together, and in alternation with those of the other pair when it is used.

<sup>1</sup> Dr. Harrison Allen (*Memoirs for a Memoir on Animal Locomotion*, 1888, p. 37) divides the gaits of quadrupeds differently, and apparently with reference to the order of innervation of the limbs in motion; that is, in accordance with their mode of co-operation. From this point of view Dr. Allen refers all gaits to two types, *synchiry* and *heterochiry*. In the former "the right and left foot of a single pair act together," whether synchronously or alternately. In *heterochiry*, locomotion is accomplished by "combination of hind and fore feet."

The typical gait of this class is the run or the jump. In the second class the limbs of one side strike the ground at the same time, and alternate with those of the opposite side. This class is represented by the pace. In the third kind of locomotion the opposite feet of different pairs strike the earth together, the line of identical movement being diagonal to the long axis of the body. The trot is typical of this kind of gait. The majority

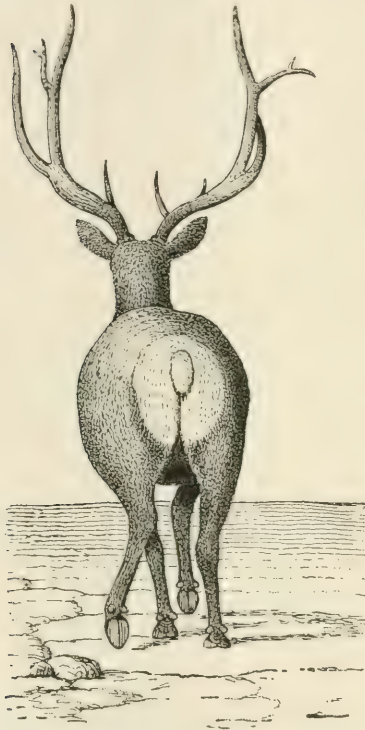


Figure 46. — *Cervus canadensis* trotting; from Muybridge, Animal Motion.

of gaits do not conform precisely with these definitions, two feet rarely striking the ground at actually the same moment, but their mechanical action can be shown to be predominantly or entirely of the three kinds. The effects of such action are as follows. In the simultaneous elevation and depression of the limbs of one pair, alternating with similar movements of the other pair, no torsion of the vertebral column results. In the alternate elevation and depression of the limbs of one side in co-operation, the vertebral axis is alternately depressed and raised again throughout its length on one side at one time. It is rapidly rocked from one side to the other during the pace and similar

gaits, and here, also, there is no torsion. When the column is supported on opposite sides at its two extremities, as in the trot, it is rocked in opposite directions at the extremities. Thus, when one side is elevated anteriorly, it is depressed posteriorly, and *vice versa*. This motion produces torsion of the column, and especially of that portion which is free from fixed connections and braces, viz. : the lumbar region. Now an examination of the gaits of animals shows that it is those which trot

which display the involuted zygapophyses, viz.: the higher Diplarthra. These animals have other gaits also, but they can and very usually do, trot. The mammals which do not display this character of zygapophyses rarely or never trot. Thus the Carnivora pace and run. The Proboscidea pace. In some of the mammals of small size the trot may be observed, as in some Rodentia, but in some of these at least we can conceive that their insignificant weight does not permit sufficient strain to affect the form of the osseous material. From the standpoint here adopted, we must suppose the Creodonta to have used the trot as their principal gait. (See Plate IV., Fig. 1, lumbar vertebra of Mesonyx.)

I refer here to an exception to the above rule which I cannot satisfactorily explain. While Carnivora are pacers, the Canidæ are to a considerable degree exceptions to the rule. They trot, or more frequently employ a gait between a pace and a trot; *i.e.* in which the feet of one side are raised consecutively, yet not so as be synchronous with those of their diagonal opposites as in a trot. Since the Canidæ are the ancestral Carnivora, and nearest the Creodonta, (having close relations with the Miacidæ), it is natural that they should retain more or less of the trot of that suborder. The involution of the zygapophyses has however entirely disappeared, a peculiarity which has yet to be accounted for.

Although the cervical vertebræ of Mammalia undergo considerable torsion, their zygapophyses are flat. But the torsion has little force, from the fact that these vertebræ sustain no lateral weight.

Besides the zygapophyses, the vertebrata possess the zygosphen, the hyposphen, the episphen, and the zygantropophysis articulations.<sup>1</sup> The zygosphen and hyposphen are nearly unknown among Mammalia, but the episphen and the zygantropophysis are found in the American Edentata. The episphen is a posterior prolongation of the roof of the neural arch above the postzygapophyses, from which it is separated by a notch. It is really a portion segmented from the roof of a zygantrum. The zygantropophysis is a prolongation of the superior surface of the postzygapophysis, and is directed posteriorly. In the American Edentata it bears an articular facet on its upper

<sup>1</sup> *Proceedings Amer. Philosoph. Society*, 1883, p. 545.



side, opposite to a corresponding facet on the lower side of the episphen. These two articulate with corresponding facets of an anterior prolongation of the metapophysis of the vertebra next posterior.<sup>1</sup> In the *Priodontes maximus* the transition between the normal articulations and those just described may be observed as we pass from the anterior dorsal region posteriorly. First the roof of the neural arch projects anteriorly beneath the arch of the preceding vertebra, forming a zygosphen of a very depressed type, combined with the prezygapophyses. The postzygapophysial surfaces are also continuous with the inferior side of the neural arch, or zygantral surface. The zygapophysial surfaces soon become distinct, but are not supported by distinct processes anterior to the last lumbar and first sacral vertebræ. The metapophyses begin to develop well anteriorly on the dorsal series, but they do not articulate with the zygantrapophysis in front of them until the sixth dorsal. On the seventh dorsal it joins a single large facet above and external to the postzygapophysis. On the eighth this facet, *i.e.* the roof of the neural canal, is deeply fissured by an uplooking ridge which separates the prezygapophysis from the zygosphen, and the episphen has its origin. On the ninth vertebra this ridge widens, and on the eleventh and twelfth it becomes distinctly part of the base of the metapophysis, which articulates above with the episphen, and below with the zygantrapophysis.

This succession of development of these articulations probably indicates the manner of their origin. Both the episphenal and zygantrapophysial articulations are due to the splitting of the roof of the neural arch on each side behind, by a keel of a zygosphenal plate which underruns the usual roof from the vertebra behind. It is a significant fact that this splitting, *i.e.* the development of the angular ridge on each side the zygosphenal roof, first appears in both the anteater and armadillo, on the first vertebra which is disconnected with the sternum, or without hæmapophysis; and which is therefore susceptible of the greatest amount of vertical movement. The prolongation of this ridge is really the prolongation of the base of the metapophysis.

We can now, I believe, associate this peculiar vertebral structure as an effect with anteroposterior strains as a cause, in these

<sup>1</sup> Flower, *Osteology of the Mammalia*, 1885, p. 62.

animals. In the first place, the effect is not due to the metapophysis, but to the anterior extension of their bases. This is demonstrated by the fact that the articulations are equally developed in the anteater and in the armadillo, although in the former animal the metapophyses have not the enormous length that they have in the latter. That they are due to anterior extension of the base is shown by the fact that in various mammals where they are developed as largely as in the anteater (*e.g.* the mole), but where they have the usual position, the additional vertebral articulations do not exist. In *Talpa europæa* the metapophysis overlaps the neural spine of the vertebra in front of it very little. In both *Myrmecophaga bivittata* and *Priodontes maximus* its anterior extremity is opposite the anterior border of the neural spine of the vertebra in front. The anterior transference of the metapophyses could then only have been accomplished by longitudinal muscular strain. This would be produced by strong upward curvature of the column, especially of its lumbar region, and strain on the intervertebral ligaments and muscles. The zygosphenal arched plate would be thus produced, its effect being to protect the spinal cord, while the neural arches were strained apart. The metapophysis, as an important muscular insertion, would be subjected to an anterior drawing strain, which would cause its base to advance with the advance forwards of the neural arch, and finally to notch, and at last to divide the arch in front of it, by pressure caused by its apex on the straightening of the column, thus cutting off the episphen. This action would be distinctly aided by the increasing width of the metapophysis at the base, which spreads the zygapophysial faces outward and produces a longitudinal angle in the lateral parts of the surfaces in contact, cutting off the zygosphenal from the zygantral surfaces.

We find that just such flexure of the vertebral column as is above inferred, is a characteristic habit of most Edentata, especially of the anteaters, armadillos, and pangolins (Manidæ). They roll themselves into a ball-like form, and retain the position against attack with great energy. But here we are confronted by the fact that the Manidæ possess this habit, and yet totally lack the complex vertebral articulations of the American Edentata (Xenarthri). If we refer the energetic flexures of the vertebral column to fossorial habits, we are met by the same

difficulty; the *Manidæ* are very similar in this respect to the Anteaters. The same is true of the African *Orycteropus*. In spite of this embarrassing circumstance, I cannot but think that the explanation of the xenarthrous structure above offered is the correct one, and we only require more knowledge of the phylogeny of the Old World *Nomarthra*, and of the habits of all the forms, to learn the cause of this discrepancy. One of several possible explanations may turn out to account for it. Such might be the recent adoption of the habit of rolling on the part of the *Manidæ*; or the feebleness of the species of that family forbidding their growth energies to respond to the stimulus. Or, on the other hand, the existence of some habit of vertebral flexure in the ancestors of the existing *Xenarthri*, which is unknown to us, may be the cause.

#### 4. THE SCAPULAR ARCH.

There is a close relation between the condition of the Mammalian clavicle and the use of the anterior limb. As a primitive element of the vertebrate skeleton, *Mammalia* naturally inherit it from their reptilian ancestors. Its absence in many of the former may be attributed to disuse. The use of the clavicle is to strengthen the scapular arch in the transverse direction; that is, against lateral strains both of pulling and pushing, which come almost entirely from the use of the anterior limbs. In *Mammalia*, where the use of the limbs, and consequently the direction of strain, is vertical, the clavicles are wanting, as in all *Ungulata* except *Quadrumania*. (The condition of the *Condylarthra* as to clavicle is unknown.) In digging mammals the clavicles are generally developed directly as the fossorial power, and especially as the manner of digging is horizontal or vertical. In the mole the digging is horizontal, and here the clavicle is excessively wide and short. In the armadillos, where the movement of the fore legs is vertical, the clavicles are both long and stout. In *Carnivora* the clavicle is rudimental, but where present the species are vertical diggers. In types of aquatic habit clavicles are wanting. Such are the insectivorous genus *Mythomys*, the otters, seals, and the *Cetacea*. These animals all have more or less lateral movement of the fore legs, but the resistance of water, the medium in which they move, is greatly less

than that of the earth. In the case of the *Quadrumana* the movements of the fore legs are much varied, but include many transverse strains. The use of these limbs in swinging the body in all directions when climbing, furnishes ample use for a clavicle, and cause sufficient to prevent its atrophy.

##### 5. THE PELVIC ARCH.

Modifications of the pelvic arch in *Mammalia* are seen chiefly in the form of the ilium and the direction of the pubis.

The ilium differs in regard to the expansion of its proximal part, and the consequent length of its crest. It is a narrow bone in *Marsupialia* and *Rodentia*, and is a little wider and more flattened in *Carnivora*. In *Edentata* and *Quadrumana* it is considerably expanded, but the greatest expansion is seen in the *Ungulata* which are not *Taxeopoda*. There is a direct relation between the form of the iliac plate and the weight that it has to bear. In the mammals with narrow ilium the abdominal viscera are light as a consequence of either relatively or absolutely small size. In the types with wide ilia, these bones support weight either (1) with the length of the crest; or (2) with the long axis of the plate; or (3) transversely to the long axis. In (1) the iliac crest supports the huge belly with elongate viscera, of the *Proboscidea*, *Amblypoda*, and *Diplarthra*, all herbivorous or omnivorous. In (2) the body is erect more or less of the time, and the weight of the viscera passes downwards into the pelvis, spreading laterally against the iliac plates. In the smaller *Edentata* this pressure is insignificant, or rarely felt; but in the huge extinct forms of the order the *Megatheriidae*, the customary attitude in feeding was, as Owen pointed out, obliquely erect, leaning against the trees, or reaching upwards to obtain their branches and foliage. In the *Quadrumana*, the most constantly erect species, man, has the most widely expanded ilia. In (3), the only representation is the family of the sloths. Here the ilia bear a part of the viscera, directly, as the animal hangs suspended from the limb of a tree.

The only noteworthy peculiarity of the pubis is the posterior direction which it presents in the *Edentata*. This character is traceable to the semi-erect position of the ancestors of the



present forms, the *Megatheriidæ*. Their long pubis has been generally pressed downwards and backwards by the weight of the viscera, while the short pubis of the *Quadrumana* has not experienced any such change of direction. The relation of this effect to the cause in question is demonstrated by the history of the *Dinosauria* and of the birds. In the former, the direction of the pubis has become downwards and then backwards, directly as the animals have more or less entirely adopted the erect attitude, by walking on their hind limbs. The viscera have been gradually swung backwards from in front of to below the point of suspension, the acetabulum, by the force of gravity; and with the advent of complete bipedism, in the birds, a part of them have moved even posterior to this point, thus more perfectly maintaining the balance in progression.

A similar posterior direction of the pubis exists in the *Talpidae*. We may with some probability ascribe this to the constant pressure on the abdomen upwards and backwards, which their mode of life entails on them. The viscera and pelvis are depressed by superincumbent weight, and the forward movement of the body in progression furnishes the pressure in the posterior direction.

### III. THE DENTITION.

The distinction of teeth into incisors, canines, and molars appears independently at various points in the line of *Vertebrata*. Incisors and molars are distinguished in *Sparoid* fishes, and in *Placodont* and *Diadectid* reptiles. Canine-like teeth, or pseudo-canines, appear in *Clepsydropid* and *Crocodylian* reptiles, and in *Saurodont* fishes. Canine-like incisors appear in the *Clepsydropidæ*. The variety of character in these structures presented by the *Mammalia* to be considered here is great, and the principles deduced from observation of them are applicable to the *Vertebrata* in general.

As mechanical causes of the origin of dental modifications, I enumerate the following:—

I. Increase of size of a tooth, or a part of a tooth, is due to increased use, within a certain maximum of capacity for increased nutrition.

II. The use and change of direction of a tooth take place

away from the direction of greatest, and in the direction of least resistance.

III. It follows, from their greater flexibility, that crests of crowns of teeth yield to strains more readily than do the cusps.

IV. The increase in the length of crests and cusps in all directions, and therefore the plications of the same, is directly as the irritation from use to which their apices and edges are subjected, to the limit set by the destructive effects of such use, or by the recuperative energy of nutrition.

V. The direction of growth of the branches of a V, or of the horns of a crescent, will be the direction of movement of the corresponding parts of the opposite jaw.

#### I. THE ORIGIN OF CANINE TEETH.

The origin of canine, pseudocanine, and canine-like incisor teeth is due to the strains sustained by them on account of their position in the jaws at points which are naturally utilized in the seizing of prey, or the fighting of enemies. In some reptiles (*Dimetrodon*) the end of the muzzle has been utilized; in *Crocodyles* the side of the jaw; while the intermediate position has been most used by *Mammalia*. The reason why the canine instead of the incisor teeth have been selected by carnivorous *Mammalia* for prehensile purposes is not at present clear to me. In accordance with Rule I., its increased size has been due to the especial and energetic strains to which it has been subjected while in use as a prehensile or offensive weapon, when buried in the body of its prey or enemy. The superior canine would acquire larger size earlier in time than the inferior canine, since it bears the greater part of such strain, as attached to the more fixed head and body of its possessor. The anterior teeth of the lower jaw would be less available for use, since they offer weaker and less fixed resistance to the opposing body. That the first tooth behind the canine was not generally enlarged is (under I.) due to the fact that its posterior position prevents it from having the same amount of use, and experiencing the strain that a tooth more anteriorly placed necessarily receives. It is excluded from considerable use by the projecting muzzle above and in front of it.

That the increased size of canine teeth is due to strains is

strongly indicated by the huge development of these teeth in the walrus. This animal uses its canines for the breaking of ice, and for lifting itself from the water onto the edge of strong ice. The fact that canines and not incisors have been thus developed is a necessary result of the fact that the walrus is a descendant of a line of animals which had already reduced incisors and larger canines.

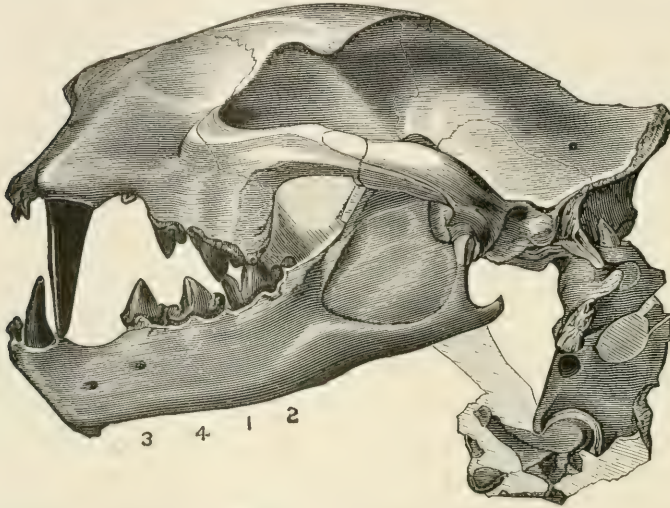


Figure 47.—*Nimravus gomphodus* Cope, two-fifths nat. size; left side of skull; from Miocene of Oregon.

## 2. DEVELOPMENT OF THE INCISORS.

The history of the incisor teeth of the Mammalia exhibits three processes; viz.: hypertrophy (*e.g.* Rodentia), specialization (*e.g.* Galeopithecus, Lemuridæ), and atrophy (*e.g.* Boöidea, Phacochoerus, etc.).

Of hypertrophy we have two types: the first represented by the Rodentia, Multituberculata, Tillodonta and their ancestors; and second, by the Proboscidea, the narwhal and certain Sirenia. As the uses of the incisors present two types corresponding with their structure, we have ground for believing the uses in question to have been the efficient agent in producing the latter. *Esthonyx* furnishes us with an example (Fig. 48) where all the incisors are present in the lower jaw, and where the function of one pair of them (the second) has evidently been partially rodent



in character; that is, it has served as a scraper and gouger of food substances. Persistent use has apparently developed the size of this pair of teeth, until we find in *Psittacotherium* (Fig. 49), they have reached a greater efficiency, and that the external incisors of the lower jaw have disappeared. This disappearance can be accounted for on the ground of disuse, a retirement from service due to position, and the increased growth of incisor No. 2. In *Calamodon* (Fig. 85) the first incisor has become rudimentary from the same cause, and in *Anchippodus* it has disappeared altogether, leaving a truly rodent incisor dentition, consisting of the second incisors only, in the lower jaw. Continued use as chisels has developed these teeth to the great proportions seen in such Rodentia as *Castoroides*, etc. (Fig. 86).

The use which the Proboscidea and Sirenia (*Halicore*) give their incisors, is, from a mechanical point of view, like that which the Carnivora give their canines; that is, it consists of strains transverse to the long axis of the tooth. The elephants

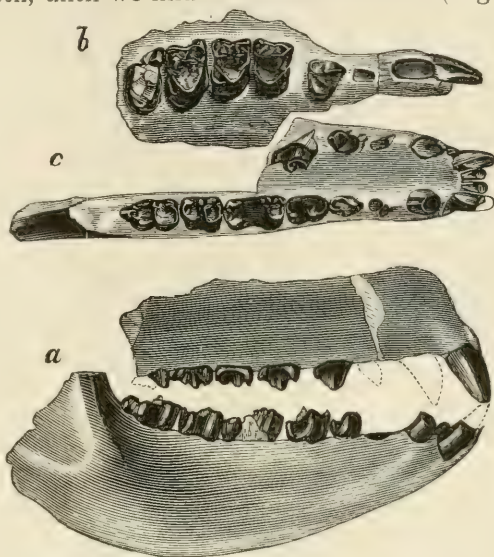


Figure 48. — *Esthonyx burmeisteri* Cope, dentition: *a*, profile; *b*, superior; *c*, inferior dentition, grinding faces. Reduced.

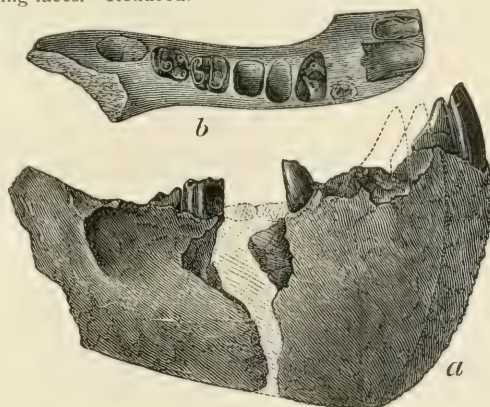


Figure 49. — *Psittacotherium multifragum* Cope, mandibular ramus, one-half nat. size: *a*, profile; *b*, from above.



use their tusks for prying up the vegetables on which they feed, or for pushing aside the vegetation through which they wish to pass. The ancestors of the Proboscidea are not certainly known, but they possessed incisors of enlarged proportions, such as we find in the Toxodontia and other late representatives of some of the primitive Ungulata. Use of such teeth in the manner referred to, without opposition from the inferior incisors, will account for the tremendous proportions which they ultimately reached in some of the species of *Elephas*.

The use made by the narwhal of its single huge superior incisor, that of an ice-breaker, indicates the origin of its large dimensions, and its primitive limited use in proportion to its small beginnings. So with the straight incisors of the hippopotamus; use as diggers has straightened them to a horizontal from their primitive vertical direction, a change partially accomplished in the true pigs (*Sus*.)

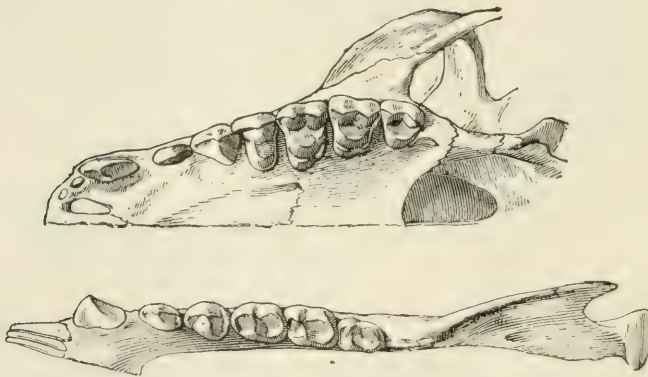


Figure 50.—*Lemur collaris*, dentition from below and above; nat. size; original.

In the Sirenian genus *Halicore* the upper incisors have been used in excavating vegetable growths from the banks and bottom of shallow seas. The transition from three incisors (*Prorastomus*) to two (*Dioplotherium*), and to one (*Halicore*), is identical with what has taken place in the Proboscidea and Rodentia, and has resulted in the production of an effective digging tool. In other genera, whose habits of browsing on soft growing materials did not necessitate the use of digging incisors, these teeth became atrophied, as in the manatee and *Rhytina*.

The inferior incisors of the true lemurs are straight, horizontal,

close together, and of slender form. The canines form part of the series, and are not distinguishable by external characters from the incisors. The reason of the peculiar characters displayed by these teeth is to be found in their present habits. These organs are used as combs for dressing the fur, and for removing parasites from the skin, and the apparatus is a most effective one. The gradual evolution of this character and its accompanying function may be traced from the *Adapidæ* of the Eocene period. In some of these forms (as *Tomitherium*) the incisors are quite oblique, and in *Adapis* the canines are incisiform. The mechanical effect of combing the hair with incisors of ordinary structure, would be to first wear off any lateral expansions of the crowns, and then to narrow their apices. The strains would also gradually cause a successively procumbent, and then decumbent direction of the crowns. Lack of use, owing to lack of opposition of the inferior incisors, would be followed in the superior incisors by the reduction in size which characterizes them. I have not seen *Galeopithecus* in life, but I suspect that its very peculiar comb-like inferior incisors are the product of a similar habit. In this genus, however, the incisors have transversely expanded crowns, and they are divided from the edge to near the base by parallel fissures. Thus is produced a comb, which is as effective functionally as is that of the Lemurs. I suspect that this result was brought about by use, on the part of the ancestors of this genus, of incisor teeth already so expanded as to suffer division rather than contraction by the long-continued friction of hair.

The atrophy of incisors is a fact for which mechanical reasons are not readily found. It has occurred in the higher *Amblypoda* (Fig. 66) and *Artiodactyla*, and in some of the *Perissodactyla* (*Menodontidæ*, Fig. 81), as well as in the *Edentata*. In the three groups first named, this loss has been accompanied by the development of horny processes on the skull, and this modification, occurring on three so diverse groups of *Ungulata*, excites the suspicion that there is some necessary connection between the two phenomena. I have suggested that the atrophy of the incisors in these cases was due to the abstraction of growth energy and material, from the premaxillary region, for use in horn-building. But there is no demonstration as yet attainable that such is a dynamic law. The loss of the incisors

in the wart hog and in the lower jaw of elephants may be associated with the great development of the canine and molar teeth in the former, and of the superior incisors in the latter. This can be only regarded as a surmise in the present state of knowledge. In bats loss of median incisors may be ascribed to disuse, as they certainly can have had, for a long time, very little functional value. Of the loss of incisors it can be only said that it is most easily accounted for by disuse, since the molars are naturally preferred for mastication of the soft vegetable food on which those animals live, owing to their enclosed position in the mouth. But why the Edentata should have lost inferior incisors, while Artiodactyla retained them, is not clear, excepting in the case of genera like *Diadomus* with approximated canines.

### 3. DEVELOPMENT OF MOLARS.

In fishes and reptiles where teeth occasionally present very primitive conditions, the theory of the origin of particular types of molar teeth is more simple than in the case of Mammalia. Under Rule II. direct pressure on a simple tooth crown would, if long continued, cause it to expand laterally, or in the direction of least resistance, and to grow but little in its vertical axis, *i.e.* in the direction of greatest resistance. Constant use will account for the increased size of such teeth as compared with those in other parts of the jaws.

In the case of the Mammalia, molar teeth are not traceable back to ancestral types of reptilian molars, but to simple conic (haplodont) reptilian teeth. The process of the evolution of the complex mammalian molars from these, forms the subject of the following pages.

I have already shown that the greater number of the types of this series have derived the characters of their molar teeth from the stages of the following succession. First a simple cone or reptilian crown, alternating with that of the other jaw (haplodont type). Second, a cone with lateral denticles (the triconodont type). Third, the denticles to the inner or outer side of the crown, forming a three-sided prism, with tritubercular apex, which alternates with that of the opposite jaw (tritubercular type). Fourth, development of a heel projecting from the pos-

terior base of the lower jaw, which meets the crown of the superior, forming a tuberculo-sectorial inferior molar. From this stage the carnivorous and sectorial dentition is derived, the tritubercular type being retained. Fifth, the development of a posterior inner cusp of the superior molar and the elevation of the heel of the inferior molar, with the loss of the anterior inner cusp. Thus the molars become quadritubercular, and opposite. This is the type of many of the Taxeopoda, including the Quadrumana and Insectivora as well as the inferior Diplarthra. The higher Taxeopoda (Hyracoidea) and Diplarthra, add various complexities. Thus the tubercles become flattened and then concave, so as to form V's in the section produced by wearing; or they are joined by cross-folds, forming various patterns. In the Proboscidiæ the latter become multiplied so as to produce numerous cross-crests.

The dentition of some of the Sirenia is like that of some of the Ungulata, especially of the suilline group, while in others the teeth consist of cylinders. In the Cetacea the molars of the oldest (Eocene and Miocene) types are but two-rooted and compressed, having much the form of the premolars of other Mammalia. In existing forms a few have simple conical teeth, while in a considerable number teeth are entirely wanting.

Of the two types of Monotremata, the Tachyglossidæ and the Ornithorhynchidæ, the known genera of the former possess no teeth, and the known genus of the latter possesses only a single corneous epidermic grinder in each jaw. As the Theromorphous reptiles from which these are descended have well-developed teeth, their condition is evidently one of degeneration, and we can look for well-toothed forms of Monotremata in the beds of the Triassic and Jurassic periods. Perhaps some such (the Multituberculata) are already known from jaws and teeth. In the marsupial order we have a great range of dental structure, which almost epitomizes that of the Monodelph orders. The dentition of the carnivorous forms is creodont; that of the kangaroos is perissodactyle, and that of the wombats is rodent. Other forms repeat the Insectivora. I consider the placental series especially, as the evolution has been similar in both cases.

In ascertaining the mechanical causes of these types of teeth, the first essential is to ascertain the character of their movements. The following table gives a summary of them:—



- I. Inferior molars work within superior molars, but not between them. Psalidodect mastication.
1. The inferior molars shear on the interior side of the superior. Triconodontidæ.
- II. Part or all of inferior molars work between superior molars. Amœbodect mastication.
2. The inferior molar shears forwards on the superior molar. Proterotome mastication . . . . . Creodonta; Carnivora.
  3. The inferior molars shear posteriorly against the superior molars. Opisthotome mastication . . . . . Coryphodontidæ, Uintatheriidæ.
- III. Molar teeth of both jaws oppose each other. Antiodect mastication.
4. The movement of the lower jaw is vertical. Orthal mastication; Suoïdea, Tapiridæ.
  5. The movement of the lower jaw is from without inwards. Ectal mastication . . . . . many Perissodactyla.
  6. The movement of the lower jaw is from within outwards. Ental mastication . . . . . most Artiodactyla; some Perissodactyla.
  7. The movement of the lower jaw is from before backwards. Proal; most Rodentia.
  8. The movement of the lower jaw is from behind forwards. Palinal; Proboscidea (Ryder).

The methods of mastication of Division I. may be also defined by the terms of Division II. Thus the proterotomes are all orthal, and the opisthotomes are ectal. Some of the orthals are opisthotome, as the Tapiridæ.

#### 4. ORIGIN OF THE TRICONODONT MOLAR.

The triconodont molar is the earliest example of a process which has been frequent in the history of the Mammalia, viz.: the appearance of cusps or folds at the base of the crown of the tooth. It is, in the case of the early Jurassic Mammalia which exhibit it, the Triconodontidæ, intimately connected with the final distinction of the roots of the molars. The ancestors of this family are probably the Dromotheriidæ of the Trias, in which the separation of the roots is only indicated by a groove,<sup>1</sup> a state of things already observed in a species of the Permian genus of Reptilia, *Dimetrodon* (Cope). The three or four small denticles of *Dromotherium*, are replaced by one in front of and one behind the principal cusp, in *Triconodon*. No mechanical cause can be assigned for the development of these cusps, but

<sup>1</sup> See Osborn, *American Naturalist*, Dec., 1888.

the nutrition of the parts probably has had an important influence on the process. Each basal cusplet stands nearer to the point of entrance to the crown of the nutritive artery which ascends — or descends through the root — than any other cusplet, and would therefore grow more rapidly than any other secondary part of the crown under the stimulus of use. The basal cusplets have thus replaced those occupying more elevated positions on the principal cusp, and ultimately in some groups equal it in dimensions; as in the true inferior sectorial of Carnivora, and in quadritubercular types.

##### 5. THE ORIGIN OF THE TRITUBERCULAR MOLAR.

The anterior cusplet of the triconodont crown has been called in the upper jaw the paracone, and in the lower jaw the paraconid; and the posterior cusplet is the metacone or metaconid, respectively. These cusplets serve to fill up the spaces between the teeth, and thus to produce a certain amount of interference

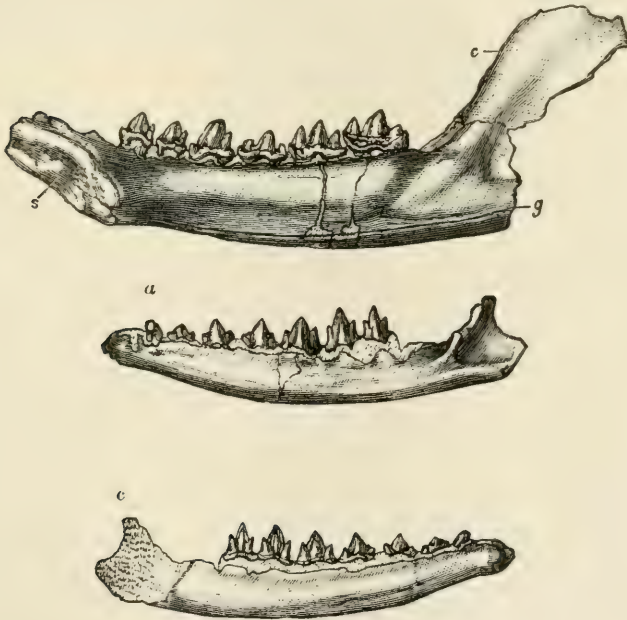


Figure 51. — *Triconodon ferox* Marsh, inner side of ramus; three times natural size: *g*, mylohyoid groove.

Figure 52. — *Menacodon rarus* Marsh: *a*, outer, *c*, inner, side of ramus, three times nat. size; all from Jurassic beds of Wyoming; from Marsh.

between those of opposite jaws. As the lesser cusps are the less resistant to the wedging pressure of such contact, their position would change under its influence, rather than the large central cusps. The lower jaw fitting within the upper, the effect of the collision between the cusplets would be to emphasize the relation still more; that is, the cusplets of the upper jaw would be wedged outwards, while those of the lower jaw would be pressed inwards, the major cusps retaining at first their original alternate position. With increase of the size of the teeth the cusps would soon assume in each jaw a position more or less transverse to that of the other jaw, producing, as a result of the crowding, a crown with a triangular section in both. The process may be rendered clear by the following diagram:

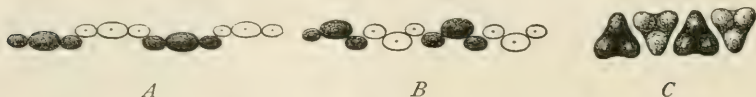


Figure 53. — Diagrammatic representations of horizontal sections of tricuspidate molars of both jaws in mutual relation; the shaded ones represent those of the upper jaw: Fig. A, Triconodon; Fig. B, Menacodon; Fig. C, ideal tritubercular molars, approached by Menacodon, Fig. 52.

The first modification of the tritubercular molar of the lower jaw is the addition of a low cingulum at the posterior base. This is seen in a rudimentary condition in various living species of the Centetidæ and Chrysochlorididæ of the Insectivorous order (Fig. 56); but in these existing forms the superior molar has added a posterior cingulum also, which widens internally, or towards the palate (Fig. 54). In the evolution of the dentition, the inferior posterior cingulum, or "heel," was developed first, as in the *Deltatherium*, *Centetes*, and *Stypolophus* (Figs. 54, 56, 58), where it is quite large; while the superior cingulum is wanting in *Stypolophus* and *Didelphodus*, but is present in a very rudimentary condition in *Deltatherium fundamini*. In all of these genera the external cusps of the superior series have been pressed inwards, and more or less together, and are therefore removed in this respect from the primitive condition. The more primitive state of the superior cusps is seen in some species of *Miocænus*, where, however, the posterior cingulum is developed. The primitive type of tritubercular superior molar is that of *Sarcothraustes*, and in the same genus the inferior molar only

differs from the primitive type in having a well-developed heel. Among recent Mammalia the carnivorous and insectivorous Marsupialia generally have the tritubercular lower molar with heel. In the Chiroptera and many Insectivora the heel is largely developed, and supports two cusps, as it does in some Creodonta.

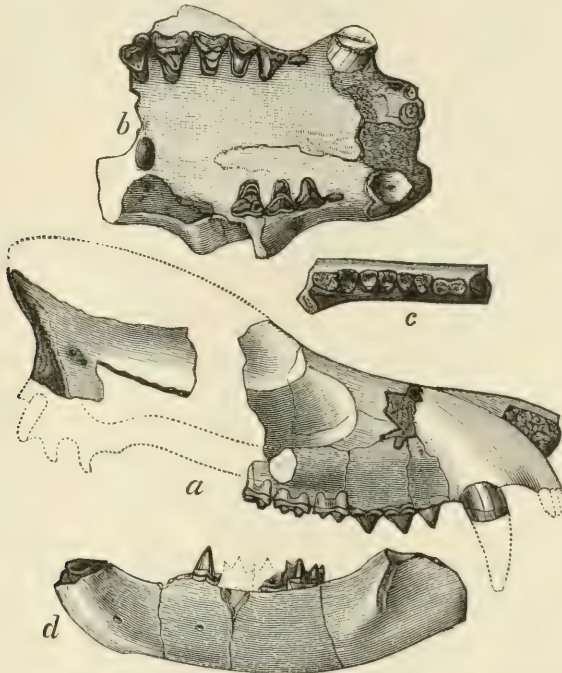


Figure 54.—*Deltatherium fundaminis* Cope, fragmentary skull; two-thirds nat. size; from the Puerco bed of New Mexico. Figs. *a*, *b*, *c* from one individual; Fig. *d*, from a second animal; Fig. *a*, right side of cranium; *b*, palate from below; *c*, mandible, part from above; *d*, left ramus, outer side; from the Report of the U. S. Geol. Surv. Terrs., Vol. III.

From this point the evolution of the tritubercular molar must be considered from two standpoints. The first is the mechanical cause of the changes of its form; and the second is the mechanical cause of its definite location in a particular part of the jaw. For it has been already stated that in the evolution of the sectorial dentition of the Carnivora, the number of molars and premolars has considerably diminished.

In the tritubercular dentition the crowns proper of one jaw alternate with those of the other (Fig. 56); but when heels are added in either jaw, they will oppose such part of the crowns of



the teeth in the opposite jaw as comes in contact with them when in use. The development of the heel in the inferior molars produced a type which is known as the tuberculosectorial. This type characterizes the Creodonta and a few Carnivora. In the former there are generally three such teeth, in the latter but one.

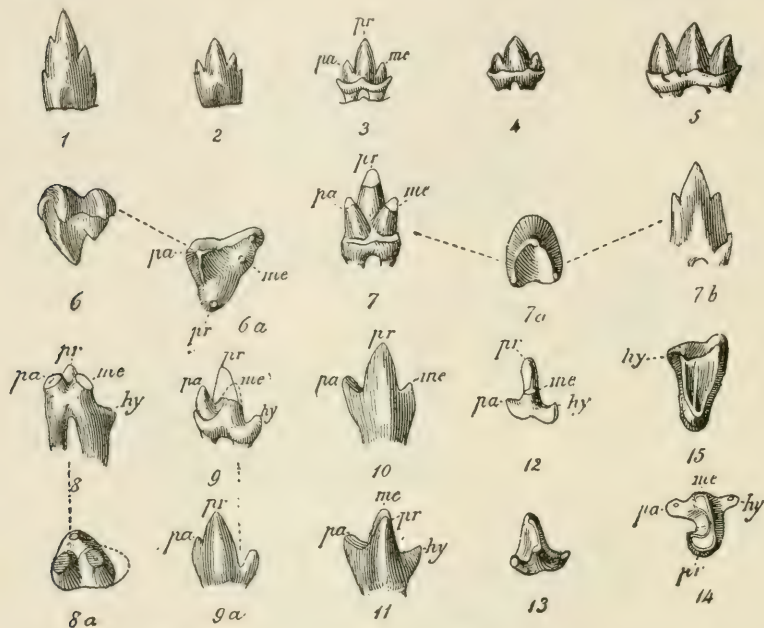


Figure 55. — Molars of Triassic and Jurassic Mammalia, enlarged; from Osborn: 1, Dromotherium; 2, Microconodon; 3, Amphilestes; 4, Phascolotherium; 5, Triconodon; 6, Peralestes; 7, Spalacotherium; 8, Amphitherium; 9, Peramus; 10, Asthenodon; 11, Dryolestes; 12, 13, Amblotherium; 14, Achyrodon; 15, Kurtodon; all inferior molars except Figs. 5, 6, and 15.

## 6. ORIGIN OF THE TUBERCULOSECTORIAL MOLAR.

In this type of inferior molar the primitive tritubercular part of the crown stands principally anterior to the posterior root of the tooth. It appears that the posterior root has been extended backwards, so as to occupy a position below the middle of the superior molar, while the tritubercular crown has been confined to the space between the crowns of the superior molars. This would follow of necessity from the alternating action of the crowns of the opposite series, in connection with a general increase in

size of the teeth. In the opening of the jaws in a Creodont, the elevated portion of the inferior crown shears by its posterior face against the anterior face of the superior molar, thus re-

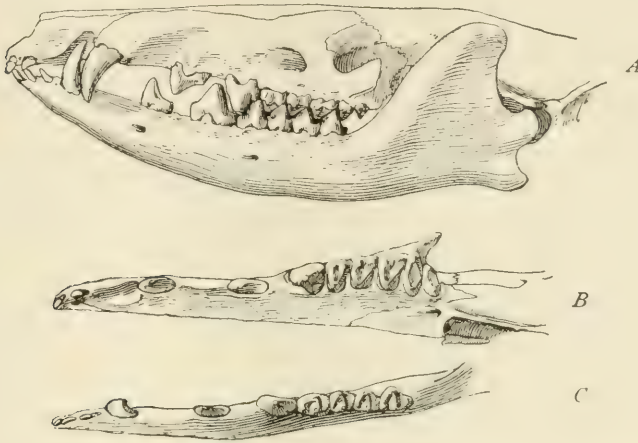


Figure 56.—*Centetes ecaudatus*: A, skull, side seen obliquely from below; B, superior molars from below; C, inferior molars from above.

straining its extension posteriorly. The stimulus of use, however, develops a low extension posteriorly, or a heel, which covers the posterior root, and opposes in mastication the internal extremity or tubercle of the crown of the superior molar above it. Thus a molar element in mastication is added to the sectorial in some Creodonta, and in Canidæ and Ursidæ, etc., among Carnivora. This function predominates over that of the anterior triangle in the Lemuridæ (Fig. 57).

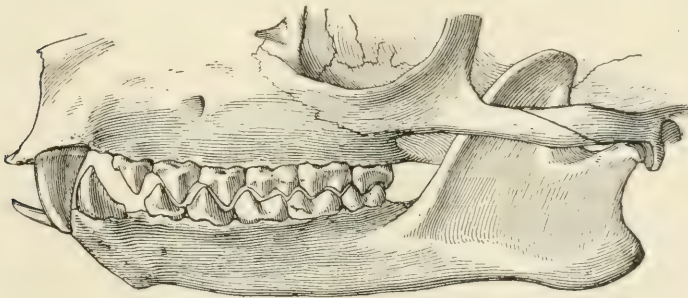


Figure 57.—*Lemur collaris*, dentition closed, showing development of heel of inferior molars; original.

## 7. ORIGIN OF THE SECTORIAL DENTITION.

The successive modifications of form which have resulted in the existing specialized single inferior sectorial tooth of the Felidæ have been already pointed out. They have been shown to consist in the gradual obliteration of the internal and posterior tubercles, and the enlargement of the two external tubercles of the primitive triangle, together with the extinction of the heel. The modification in the character of the dentition taken as a whole was shown to consist in the reduction of the number of the teeth, including the sectorials, until in *Felis*, etc., we have almost the entire function of the molar series confined to a single large sectorial in each jaw.

The genesis of the superior sectorial tooth has been explained as follows. In consequence of the fact that the lower canine tooth shuts anterior to the superior canine, the result of the enlargement of the diameters of those teeth will be to cause the crowns of the inferior teeth to be drawn from behind forwards against those of the superior teeth (Fig. 58). Thus a shearing motion would result between the anterior external edge of the lower triangle and the posterior internal edge of the

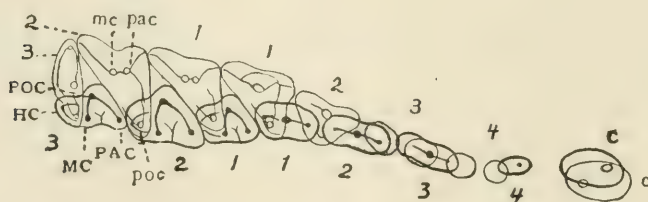


Figure 58.—*Stypolophus whitæ* Cope; diagram representing the apposition of the inferior and superior molars. The superior are in light, the inferior in heavy lines. The numbers represent the molars and premolars: *C*, canine; *poc*, protocone; *pac*, paracone; *mc*, metacone; *POC*, protoconid; *PAC*, paraconid; *MC*, metaconid; *hc*, hypocone; *HC*, hypoconid.

superior triangle. Now the characters of the true sectorial teeth consist in the enormous extension of these same edges in a fore and aft direction, the inferior shutting inside of the superior. To account for the development of these blades we must understand that the oblique pressure of the front edge of the lower tooth, on the hind edge of the superior tooth, has been continued

for a very long time. We must then observe that the internal tubercle of the superior triangle has been pushed continually forwards and been reduced to a very small size. Why should this occur? Why should not the corresponding tubercles of the inner side of the lower crown have been pushed backwards, since action and reaction are equal? The reason is clear: The superior tubercle is supported by but one root, while the resistant portion of the inferior crown is supported by two, thus offering twice the resistance to the pressure that the superior does. But why should the anterior part of the inferior tooth move forwards? even if it be in the direction of least resistance? This is due to the regular increase in size of the teeth themselves, an increase which can be traced from the beginning to the end of the series. And this increase is the usual result of use (Fig. 60).

The mechanics of the above proposition I believe to be correct, but I have had occasion to modify the statement as to the initial

cause of the process. In many primitive Ungulata the canines have been as well developed as in the Carnivora, yet the forward pressure of the inferior molars on the superiors has not resulted, or has not been sufficient to produce sectorial molars in those types. In the Amblypoda, the lower molars even shear backwards on the upper ones. It seems then that this growth of the canines is not in all instances sufficient to cause a proterotome mastication. I suspect that the more usual cause is to be found in the voluntary effort of the primitive flesh-eater, to masticate flesh by the manipulation of his lower jaw and the body to be divided. The looseness of articulation in primitive Creodonta will permit a manipulation such as we observe in various Ungulates to-day. The formation of a habit of a proterotome mastication would result, and the structural results would succeed as above pointed out.

The excess of the forwards pressure of the inferior teeth

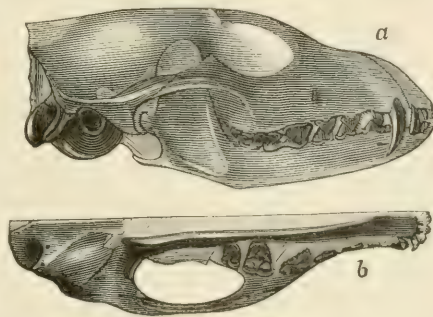


Figure 59. — *Cynodictis geismarianus* Cope; skull one-half natural size: *a*, right side; *b*, left side from below.



against the superior over any backwards pressure, has left the posterior internal cusp of the triangle of the inferior molar without contact or consequent functional use. It has, consequently, gradually disappeared, having become small in the highest Canidæ, and wanting in some Mustelidæ, and all Felidæ. The heel of the same tooth has had a similar history. With the diminution in size of the first superior tubercular, with which it

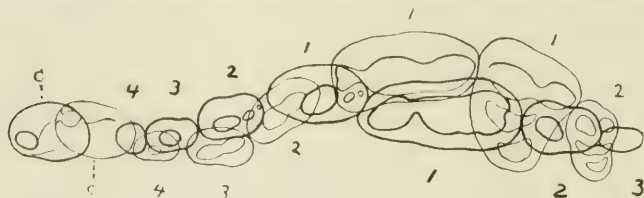


Figure 60. — *Aclurodon sævus* Leidy; diagram representing coadaptation of crowns of superior and inferior molars in mastication; lines and lettering as in Fig. 58.

comes in opposition in mastication, its functional stimulus also diminished; and it disappeared sometimes a little sooner (Felidæ) and sometimes a little later (Hyænidæ) than that tooth.

The specialization of one tooth to the exclusion of others as a sectorial, appears to be due to the following causes. It is to be observed in the first place that when a carnivore devours a carcass, it cuts off masses with its sectorials, using them as shears. In so doing it brings the part to be divided to the angle or canthus of the soft walls of the mouth, which is at the front of the masseter muscle. At this point the greatest amount of force is gained, since the weight is thus brought immediately to the power, which would not be the case were the sectorial situated much in front of the masseter. On the other hand, the sectorial could not be situated farther back, since it would then be inaccessible to a carcass or mass too large to be taken into the mouth.

The position of the sectorial tooth being thus shown to be dependent on that of the masseter muscle, it remains to ascertain a probable cause for the relation of the latter to the dental series in modern Carnivora. Why, for instance, were not the last molars modified into sectorial teeth in these animals, as in the extinct *Hyænodon*, and various *Creodonta*. The answer obviously is to be found in the development of the prehensile character of the canine teeth. It is probable that the gape of the

mouth in the Hyænodons was very wide, since the masseter was situated relatively far posteriorly. In such an animal the anterior parts of the jaws with the canines had little prehensile power, as their form and anterior direction also indicates. They doubtless snapped rather than lacerated their enemies. The

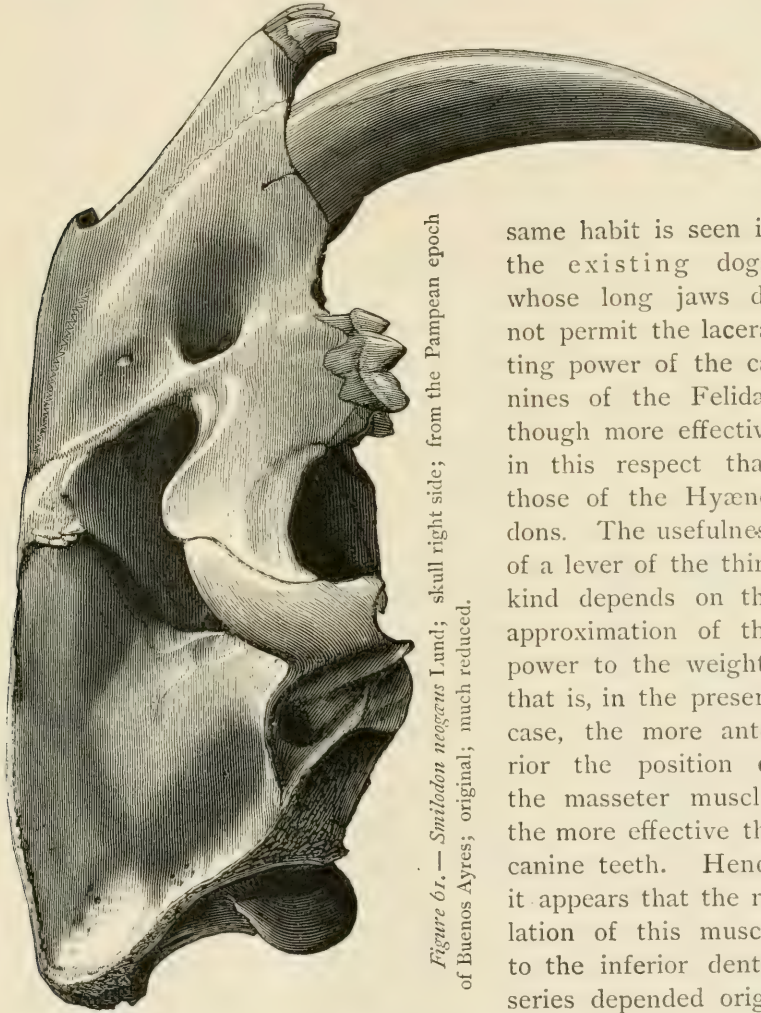


Figure 61. — *Smilodon neogaeus* Lund; skull right side; from the Pampean epoch of Buenos Ayres; original; much reduced.

same habit is seen in the existing dogs, whose long jaws do not permit the lacerating power of the canines of the Felidæ, though more effective in this respect than those of the Hyænodons. The usefulness of a lever of the third kind depends on the approximation of the power to the weight; that is, in the present case, the more anterior the position of the masseter muscle, the more effective the canine teeth. Hence it appears that the relation of this muscle to the inferior dental series depended origi-

nally on the use of the canines as prehensile and lacerating organs, and that its relative insertion has advanced from behind forwards in the history of carnivorous types. Thus it is that the only accessible molars, the fourth above and the fifth

below, have become specialized as sectorials, while the fifth, sixth, and seventh have, firstly, remained tubercular as in the dogs, or, secondly, have been lost, as in hyænas and cats.

The reduction of the number of molars in relation to the increase in the size of the canines commenced as early as the Jurassic period.<sup>1</sup> It is seen in the genera *Triconodon* (Owen) and *Paurodon* (Marsh), where the canines are large and the molars few. In the *Plagiaulacidae* a similar relation is seen between the development of the incisors and the reduction in number of the molars. This is the modification of relation observed in existing Mammalia of the orders Proboscidea and Rodentia, which will be mentioned later, under the head of proal dentition.

#### 8. ORIGIN OF THE AMBLYPODOUS DENTITION.

As the Amblypoda form the only order of ungulate Mammalia with tritubercular superior and tuberculosectorial inferior molars, the question has arisen in my mind why they did not develop a sectorial dentition in the same way, and for the same mechanical reasons, that the unguiculate series has done so. Having assigned certain mechanical reasons for the evolution of the sectorial teeth of the Carnivora, it is necessary to explain why the Amblypoda, which had apparently the same mechanical conditions at the start, did not eventually produce the same result.

In the first place I observe in the families *Coryphodontidae* and *Uintatheriidae* of the Amblypoda, that the shearing of the inferior molar crests against the superior molar crests, is from before backwards. In the *Creodonta* and *Carnivora* it is from behind forwards. I supposed the latter movement to be due in these animals to the wedging of the inferior canine in front of the superior canine, a movement undoubtedly sufficient to account for such a shearing, other things being equal. But in the *Coryphodontidae* the canines are greatly developed, yet the shearing of the molar crests is in the opposite direction. It is also evident that the development of the canines cannot have been the cause of the maintenance of any kind of a shear between alternating parts of molar teeth, otherwise the quadritubercular

<sup>1</sup> My attention has been called to this point by my friend, Prof. H. F. Osborn, who has recently written fully on the Mesozoic mammals, and whose nomenclature of the dental cusps is here adopted.



type of molar would not have come into existence in such families as have large canine teeth, such as the Suoid Artiodactyla. I do not for these reasons abandon the opinion that the development of the canines has not had a great deal to do with the development of the sectorial dentition. I only deny that it has been the cause of its *origin*; that is, of the anterior shearing of the lower molars on the upper, at its beginning.

The peculiarities of the Pantodont and Dinoceratous dentition may be now taken up in order, and their mechanical causes assigned so far as possible. *In limine* I take the position that the mastication of the Amblypoda was accomplished by the transverse movement of the lower jaw across the upper, and that this is, therefore, the only order in which such mastication was performed by the primitive dentition, *i.e.* the tritubercular and tuberculosectorial. That this is the type of mastication is suggested, but not proven, by the anisognathism of the dental system. But it is proven by the mark or path made by the posterior external cusp of the inferior true molar across the crown of the superior molar in the Coryphodontidæ. This cusp struck the posterior side of the rudimental anterior external lobe, and passed transversely across the crown (diagonally to the principal cross-crests), and slid up the apex of the internal cusp, producing the externally directed angle in its wear, seen in all specimens of the genera Metalophodon, Coryphodon, and Ectacodon (Fig. 63). I also suspect that this movement is ectal, since the direction of the V's of the two dental series will permit no other. An attempt at an ental movement results in a jamming of the V's into each other, and further

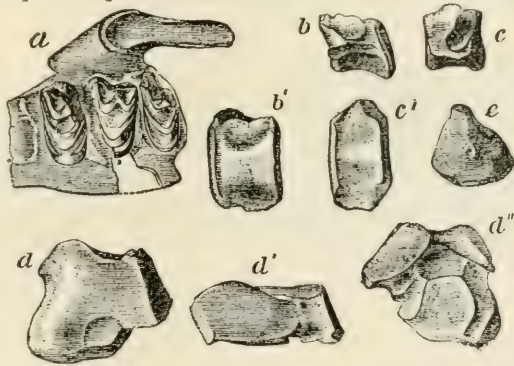


Figure 62.—Bones and teeth of *Pantolambda bathmodon* Cope, two-thirds nat. size. From the Puerco beds of New Mexico. Fig. *a*, part of maxillary and malar bones from below, showing true molars, all somewhat broken. Figs. *b* and *c*, cervical vertebrae, left side; *b'* and *c'*, do. from below. Fig. *d*, astragalus from above; *d'*, from front, showing facet for cuboid; *d''*, from below; *e*, navicular bone from below. Original, from Report U. S. Geol. Surv. Terrs., F. V. Hayden.



progress is impossible. It may be objected that the presence of the large superior canines forbids any considerable lateral movement of the lower jaw. The superior canines are, however, so divergent in the Coryphodontidæ that such movement is possible, and the transversely convex wear of these teeth proves just such a movement of the inferior canines on them. The lateral movement in the old males of the Dinocerata has been much restricted by the superior canines, but in younger males and females it was possible.

A second proposition is demonstrated by the discovery of the Pantolambididæ. This is, that the superior molars of both the Coryphodontidæ and Uintatheriidæ are derived from a type with two external V's (Pantolambda, Fig. 62), and I propose to show how this derivation has been accomplished, and under what mechanical necessity. Pantolambda also shows that the

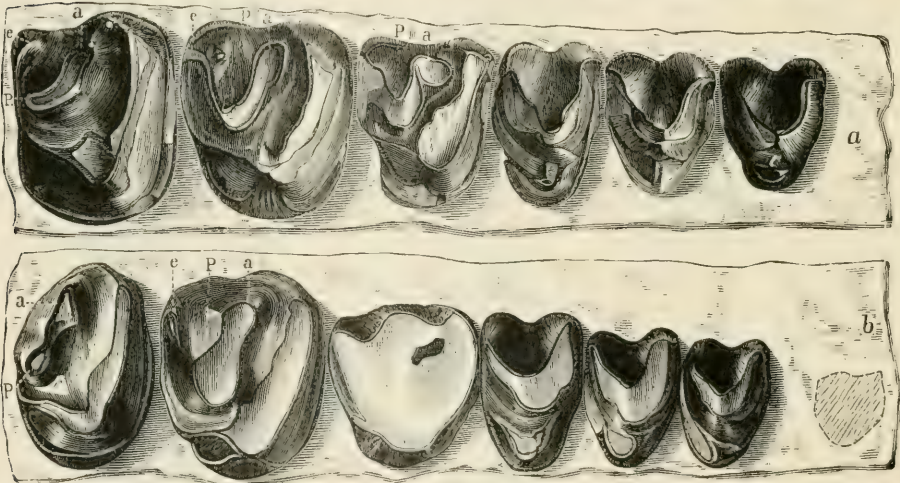


Figure 63. — Superior molar series of Coryphodontidæ, two-thirds nat. size; from the Wasatch beds of Wyoming; original. Fig. a, *Ectacodon cinctus* Cope. Fig. b, *Metalophodon testis* Cope.

inferior molar structure of the two types mentioned has been produced by the modifications of a W-shaped type of crown. I note in passing, that the type of Pantolambda is itself readily derived from the primitive  $\frac{3 - \text{tubercular}}{5 - \text{tubercular}}$  type of primitive placentals and marsupials.

With these propositions established, I proceed to consider

first the origin of the dental peculiarities of the Coryphodontidæ.

First, no posterior inner tubercle was developed on the superior molars. We may regard this as a consequence of the fact that a transverse (ectal) movement of the lower jaw was established before the appearance of this cusp, instead of after it, as was the case in other ungulate orders, and because the shearing has been always from before backwards, instead of overlapping from behind forwards, as in all other Ungulata. The stimulus already assigned as the cause of the development of the fourth tubercle is, under these circumstances, wanting (Fig. 64).

Second, the anterior cingulum, which extends from the internal cusp to the anterior external angle of the crown along its anterior base, is greatly developed. This may be reasonably ascribed to the stimulus produced by the friction of the poste-

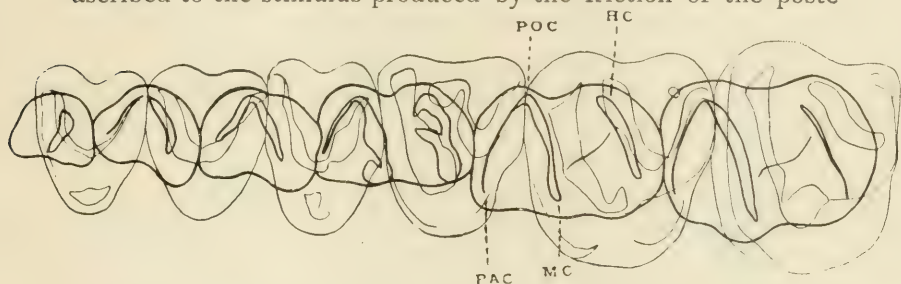


Figure 64.—Mutual relation of inferior and superior molars of a Coryphodont Amblypod. Relations and letters as in Fig. 58. The superior series is that of the *Ectacodon cinctus* Cope; the inferior, that of *Bathmodon radians* (supposed); hence the anterior V of the inferior premolars is too far anterior.

rior limb of the anterior V of the inferior molar in the transverse movement in mastication. The anterior crest of the superior molar is developed instead of the corresponding posterior crest of the superior molar in front of it, because the transverse movement of the inferior molar follows a path much more nearly coinciding with the anterior crest of the superior molar than with the posterior crest. That is, it follows a curved path of which the centre is posterior, and near or between the glenoid cavities on which the mandibular rami move, as has been described by Ryder in various other Ungulates.<sup>1</sup> This is the probable cause of the development of this crest from its origi-

<sup>1</sup> *Proceedings Philadelphia Academy*, 1878, p. 56.

nally moderate proportions in *Pantolambda* (Fig. 62), and from the unknown ancestor of that genus, where its dimensions are presumably still less considerable.

Third, the anterior external tubercle or V is reduced to a conical rudiment (Fig. 63 *a*). This is evidently due to the disuse following the great development of the anterior cingulum which extends from the internal tubercle to the anterior external angle of the crown. A similar but less considerable development of this ridge is accompanied by a corresponding reduction of the anterior external lobe, in some genera of the *Lophiodontidæ* *Perissodactyla*. The reason why this V has been extinguished and not merely pressed backwards, is the fact that the posterior external V of the superior molar has retained its place, and has not given away to allow room for the anterior one. This V has retained its place partly on account of its remoteness from the source of pressure in front, but principally because it fits the posterior transverse crest of the lower molar in front, and the anterior oblique crest of the next succeeding lower molar behind, so that its use has been only possible in its primitive position.

Fourth, the posterior limb of the posterior external V of the superior molar is wanting on the last molar in *Coryphodon*, and from the last two in *Metalophodon* (Fig. 63). The absence of this crest from the last superior molar is due to the absence of a corresponding crest of the inferior molar (Fig. 64). This is the oblique crest at the anterior extremity of the inferior molar, and it shears against the posterior limb of the posterior external V of the superior molar, representing the sectorial blade of *Carnivora*. It is little elevated in the *Coryphodontidæ*, owing to the fact that it is little used, since the crests of the inferior molars shear backwards and not forwards on those of the upper. The effect of this disuse tends, in the history of the *Coryphodontidæ*, to become more and more evident. The non-existence of a fourth molar behind the third in the lower jaw, accounts for the absence of the crest in question from the last superior molar, while the absence of the same crest from the second superior molar of *Metalophodon*, indicates the absence or rudimentary condition of the corresponding crest of the corresponding inferior molar (Fig. 65).

The above four propositions cover the principal peculiarities of the dentition of the *Coryphodontidæ*. I now proceed to a consideration of those of the *Uintatheriidæ*.



As is well known, the crowns of the superior molars in this family support two cross-crests, which converge and nearly join at the internal extremity of the crown (Fig. 66). The anterior of these crests is pretty clearly the anterior cingular crest of

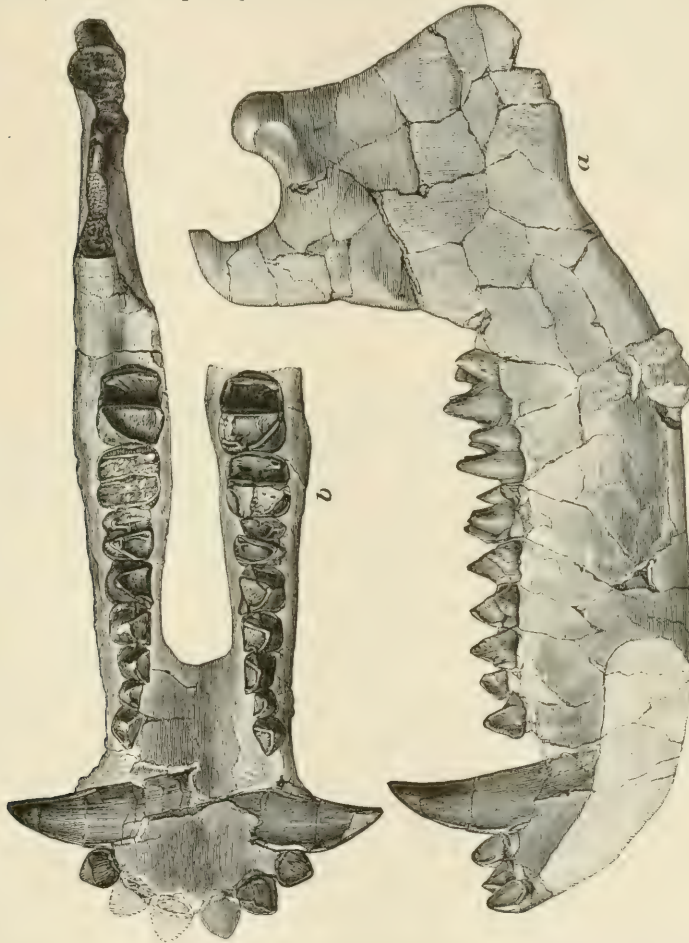


Figure 65.—*Coryphodon latidens* Cope, lower jaw, one-third nat. size; from the Wasatch epoch of New Mexico. Fig. *a*, right ramus from internal side. Fig. *b*, both rami from above. Original, from Report U. S. G. G. Surveys W. of 100th Mer., G. M. Wheeler in charge. This specimen has an anomalous premolar.

*Coryphodon*, but the homology of the posterior crest is less obvious. In order to determine this point, recourse must be had to the inferior molars, which are more readily understood.

In the lower molar of the *Uintatheriidae*, we find the anterior



triangle of the tuberculo-sectorial type, but with the anterior limb rudimental. The posterior part of the crown differs from that of the Coryphodontidæ in having no posterior transverse crest, but in its stead the diagonal crest which connects the external extremity of the posterior transverse with the interior extremity of the anterior transverse crest. This oblique crest wears the posterior crest of the superior molars on its anterior



Figure 66. — Dinocerata, teeth, one-fourth nat. size. Upper figures superior molars of *Uintatherium leidianum*, one-fourth nat. size. Lower figure, inferior molars of jaw of another species of *Uintatherium*. From Osborn, memoir on *Uintatherium* and *Loxolophodon*.

face, as the anterior transverse crest wears the anterior crest (cingular) of the superior molar on its anterior face (Fig. 67).

Comparison with the dental structure of *Pantolambda* (Fig. 62) shows which crests of the two series stand in this relation to each other. The diagonal crest of the inferior molar in this genus shears in front of the posterior limb of the anterior V of the superior molar. Guided by this fact we may regard the posterior cross-crest of the superior molar of the *Uintatheriidae*, as the posterior limb of the anterior external V.

We must then suppose that the anterior limb of this V has disappeared from this type of molar, and the anterior cingular crest has taken its place, thus forming a long V with the posterior limb. The tubercle between the crests at their open external valley, may be a remnant of this external crest. A low tubercle on the crown behind the inner extremity of the posterior crest may be a rudimental fourth tubercle (hypocone), or even the apex of the posterior external V.

The homology of the posterior crest of the superior molar here proposed, is sustained by the fact that there is no posterior transverse crest on the lower molar.<sup>1</sup> Had the crest in question been part of the posterior V of the superior molar, the posterior crest of the inferior molar would have had use, and would not have disappeared.

<sup>1</sup> The raised heel on these inferior molars is not the posterior transverse crest.

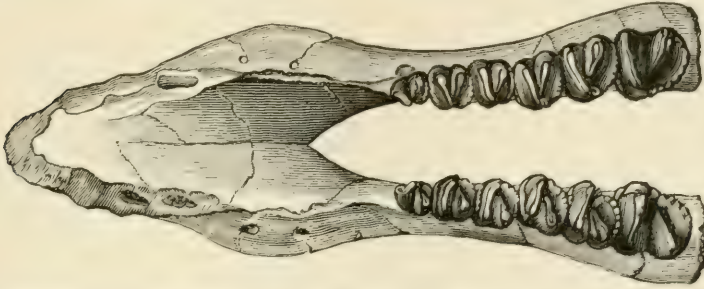
If this homology is correct, the Dinocerata were derived directly from the Pantolambdidae, and not through the Coryphodontidae.

The mechanical causes of the peculiarities of the Dinoceratous dentitions are then the following : —

First, development of anterior cingular crest ; cause same as in Coryphodontidae.

Second, loss of anterior limb of anterior external V of superior molars ; cause, disuse.

Third, shearing of oblique crest of inferior molar in front of instead of behind posterior limb of anterior external V of superior molar. Cause, development of anterior basal cingulum of superior molar, which wedges cross-crests of inferior molar anteriorly.



*Figure 67.* — Uintatherium, mandible anterior to coronoid process, one-fourth nat. size; from Bridger beds of Wyoming. From Osborn, memoir on *Loxolophodon* and *Uintatherium*.

Fourth, loss of posterior cross-crests of inferior molars. The answer to this question is the answer to the other question, Why was the oblique crest of the inferior molar developed in the Uintatheriidae while it remained rudimental in the Coryphodontidae ? The answer to these questions is the explanation of the principal peculiarities of the former family. The answer appears to me to be simply that while the movement of the lower jaw in mastication was probably ectal in the Coryphodontidae, it was probably ental in Uintatheriidae. This explanation is largely hypothetical, yet it accords with the relations between use and the development of the crests in the two families. In the ectal movement in *Pantolambda* the oblique crests of the opposing molars are soon separated from mutual contact, so that none of them have use on the internal half of the crown

except the anterior cingular. In the ental movement, on the other hand, the limbs of the external V's are used to the utmost. The posterior limb of the anterior V is most used in Panto-lambda, for the reason, as it appears to me, that the inferior molar is wedged forwards as it moves outwards in consequence of the guidance of the anterior cingular crest, and the wedge-shape of the triangular superior molar. While this causes the greatest use of the posterior limb of the anterior external V, it withdraws the posterior crest of the inferior molar from shear with the anterior crest of the posterior V, so that it has disappeared through disuse.

In general it may be observed, that the ental movement is the easier to the Dinocerata because the V's open exteriorly in both jaws. In the Pantodonta the ectal movement is easier, because the V's of the lower molars open interiorly.

#### 9. THE ORIGIN OF THE QUADRITUBERCULAR MOLAR.

The quadritubercular molar of the upper jaw was produced by the addition of a tubercle, the hypocone, at the posterior side of the internal tubercle of the original tritubercular crown. This appears first as a cingulum in the Condylarthrous family of

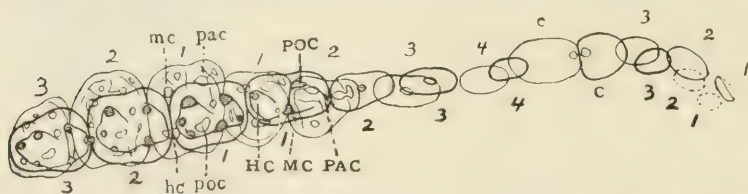


Figure 68. — *Phenacodus primævus* Cope; diagram representing relation of superior and inferior molars in mastication; lettering as in Fig. 58.

the Periptychidæ and the Creodont genus *Miocænus*, as examples. A cusp rises on the inner part of this cingulum, which is at first rudimental, as may be seen in *Miocænus corrugatus* and *Chriacus truncatus* as examples. It acquires in successive forms increased proportions, as may be seen in the Phenacodontidæ (e.g. *Phenacodus primævus*, Fig. 68). In the inferior molar the quadritubercular is formed by the loss of the paraconid, and the development of two hypoconids on the opposite angles of the heel. The paraconid diminishes *pari passu* with the increase in size of the superior hypoconid (fourth tub-

ercle), which, when it is developed, opposes the metaconid of the inferior molar. The metacone of the superior series opposes the protoconid of the inferior. Thus, although the teeth of the superior and inferior series are alternate, they do not interlock. On the contrary, they oppose each other, forming a mechanism adapted for the grinding instead of the cutting of food.

The divergence of mammalian dentition into the two types, the tritubercular and quadritubercular, has been, as it appears to me, due to the adoption of different food-habits. The tritubercular is the primitive, and is adapted for softer food, as flesh, so that primitive placental Mammalia were carnivorous or nearly so. The mastication of hard food was impossible until the molars of the two series opposed each other, and this was not accomplished until the quadritubercular superior molar was produced. This was accomplished, as I have pointed out, by the addition of a posterior internal tubercle, and I suspect that the mechanical cause of its origin was the attempt of the animal in mastication to crush substances harder than flesh against this posterior edge of the superior molar, by applying to it the anterior edge of the lower molar. In the devouring of flesh this movement is not necessary, or only necessary so far as to produce a shearing movement to cut a resisting ligament or tendon. The different mechanical movements in the two cases were due to the manipulation of its lower jaw by the animals, just as we may see them to-day endeavoring to masticate substances in accordance with their hardness, form, etc. It would appear in the case of the tritubercular superior molar, that the impact during the effort to masticate hard and tough substances, as vegetable tissues and seeds, has had its usual effect to stimulate deposit of material. The shearing movement has had an opposite effect, viz. : that of wearing away the surface subjected to it, and the flattening of the sheared face. That the development of the grinding mastication should take place in ungulate Mammalia is entirely appropriate to the structure of their digits ; the hoofed structure unfitting them for the seizure of living prey.

The completion of the quadritubercular dentition requires that the two anterior cusps and two posterior cusps of the inferior molar should reach the same horizontal plane. This involves the lowering of the anterior pair, and the elevation of the



posterior. In the species of *Miocænus* the relation of the cusps to the plane may be seen in various stages of transition. In most of them the first inferior true molar retains more or less of its elevation, which is due to the fact that the first pre-molar is always tritubercular, and leaves a triangular space between it and the first true molar.

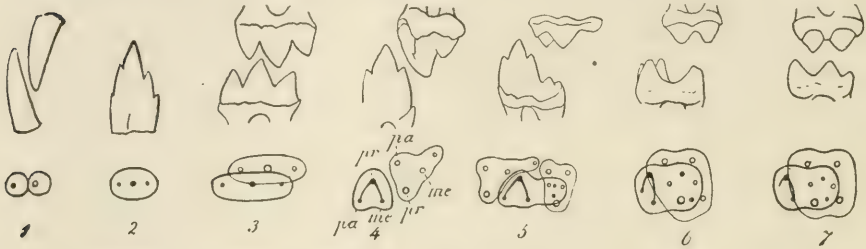


Figure 69. — Diagrams showing successive modifications of dentition from the haplodont (1) to the protodont (2), the triconodont (3), the double tritubercular (4), the carnivorous tritubercular (5), to the less and more completed quadritubercular (6, 7); from Osborn. The genera represented are: 1, *Delphinus*; 2, *Dromotherium*; 3, *Triconodon*; 4, *Peralestes* and *Spalacotherium*; 5, *Didymictis*; 6, *Miocænus*; 7, *Hyopsodus*.

The mechanical cause of this change is to be found in the relations existing between the opposing molars after the appearance of the hypocone (fourth tubercle) of the superior series. The effect of the latter when it should impinge on the para-

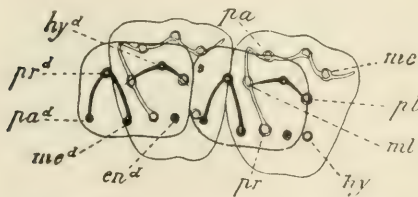


Figure 70. — Relation of the quadritubercular superior to the quinetubercular inferior molars in mastication; from Osborn, *American Naturalist*, December, 1880. *Pr.* protocone; *pr<sup>d</sup>*. protoconid; *hy*. hypocone; *hy<sup>d</sup>*. hypoconid; *pa*. paracone; *pa<sup>d</sup>*. paraconid; *me*. metacone; *me<sup>d</sup>*. metaconid; *en<sup>d</sup>*. entoconid; *ml*. metaconule; *pl*. paraconule.

conid of the inferior molar, would be to prevent contact of the heel (hypoconid) of the lower molar with the interior part (protocone) of the superior molar next posterior to it. The presence of such a slight gap would not interfere with the cracking of seeds or nuts, but would prevent the finer mastication of all substances. It is pretty clear that the mastication would

have to be performed by the anterior part of the inferior molar on the posterior part of the superior, by a dentition passing from the tritubercular to the quadritubercular condition. Such use as

it would get would probably stimulate the posterior part of the crown (heel) of the inferior molar until it should rise to meet the internal part of the superior. The more rapid wear of the paraconid and of the hypocone would bring about the general contact of the two series of molars in animals of mature age. The increased development of the heel of the inferior molar under these circumstances may have brought about the atrophy of the paraconid by appropriation of material of nutrition. But this explanation is hypothetical only. At present there is none other to offer.

#### 10. THE ORIGIN OF THE LOPHODONT MOLARS.

Quadritubercular molars have their tubercles either simple or modified into crests; to the two conditions have been applied the terms *bunodont* and *lophodont*. The component tubercles, or crests, of each tooth, may be either opposite to or alternate with each other; these conditions are termed *antiodont* and *amæbodont*, respectively. Thus all quadritubercular molars may be classified under four heads, as represented in this diagram:—

	Antiodont.	Amæbodont.
Bunodont . . . . .	* . . . .	* . . . .
Lophodont . . . . .	* . . . .	* . . . .

Two principal kinds of relation between the teeth of opposite jaws also exist, the *isognathus* and *anisognathus*. In the former the teeth of opposite jaws are of equal width, and the jaws themselves oppose each other; in the latter the teeth of the lower jaw are narrower than those of the upper, and the branches of the lower jaw embrace a narrower transverse space than the upper jaws and palate.

The problem presented by the Mammalian quadritubercular dentition is that of the derivation of the various lophodont or crested types from the simple and primitive bunodont types.

It is necessary to remember, in the first place, that teeth of the quadritubercular type no longer alternate with each other in the vertical direction; that is, those of the inferior series no longer occupy the spaces between those of the superior when the jaws are closed. In the vertical sense they oppose each other. This has been accomplished by the development of the fourth tubercle, forming an inner posterior angle of the superior

molar, which thus closes the space between its crown and that of the adjacent superior molar; and by a corresponding change in the inferior molar. In this tooth the anterior interior cusp has disappeared, and the two cusps of the heel have become elevated, so as to be on a level with the remaining anterior

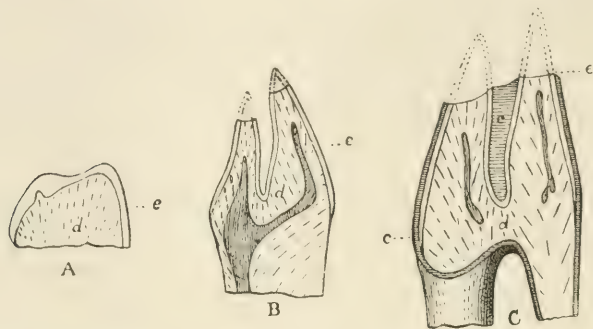


Figure 71. — Transverse vertical sections of superior molar teeth, showing transition from bunodont (1) type to lophodonts (2, 3). Fig. 1, *Sus erymanthius*. Fig. 2, *Ovis amatheus*. Fig. 3, *Bos taurus*. From Ryder, after Gaudry. Letters: *d*, dentine; *e*, enamel; *c*, cementum.

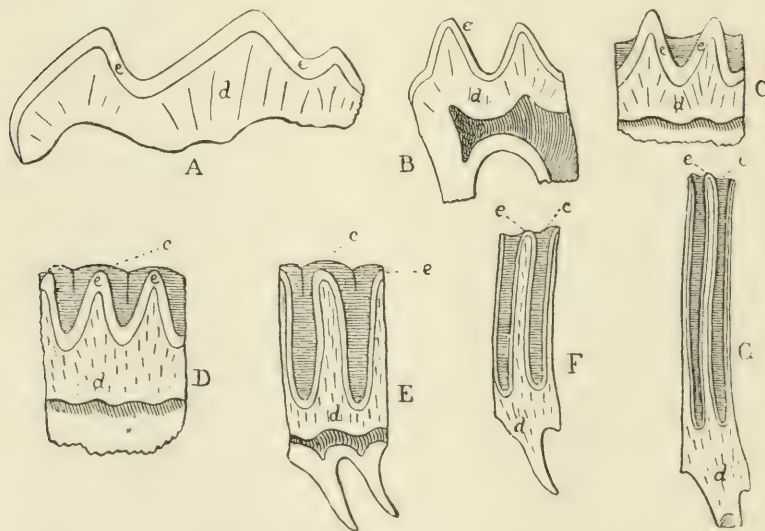


Figure 72. — Transverse vertical sections of molars of Proboscidea, showing same transition as in last figure; lettering the same. Fig. 1, *Dinotherium giganteum*; Fig. 2, *Mastodon americanus*; Fig. 3, *Elephas ganesa*; Fig. 4, *E. planifrons*; Fig. 5, *E. hysudricus*; Fig. 6, *E. indicus*.

two cusps. The result is an inferior quadritubercular molar, which opposes the superior molar which chiefly lies above it, together with a small posterior part of the superior molar in front of the latter.

It is a fact that the majority of Mammalia with bunodont dentition (the peccary, man) are also isognathous, while the majority of the lophodont types are anisognathous (tapir, ox). Striking exceptions to the latter rule are seen in the Rodentia and in the elephant. But there is evidently some connection between anisognathism and the lophodont dentition. Examina-

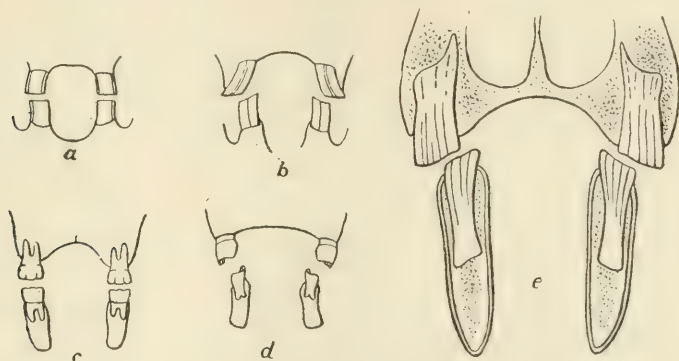


Figure 73.—Transverse sections through the maxillary apparatus of *a*, Fiber; *b*, Lepus; *c*, Dicotyles; *d*, Cervus; *e*, Equus. Figs. *a* and *c* represent isognathous dentition, and *b*, *d*, and *e* anisognathous; from Ryder.

tion shows that the anisognathous lophodonts have a different articulation of the lower jaw from that of the isognathous lophodonts. It is also found that the movement of the lower jaw on the upper in the bunodonts differs from that which is exhibited by either of the lophodont types, and that this motion is in some, but not all cases, rendered necessary by the shape of the articulation of the lower jaw with the skull. The motions of the three types may be represented as follows:—

Bunodont . . . . .	(orthal) . . . . .	vertical.
Lophodont, type one . . . .	(ectal and ental) . . . .	transverse.
Lophodont, type two . . . .	(propalinal) . . . . .	anteroposterior.

In the bunodont type the movement of the jaws in mastication is identical with that belonging to the tritubercular type, in which no other than the vertical is possible. It is rendered



necessary in many of the bunodonts by the structure of the glenoid cavity of the squamosal bone, which grasps the condyle of the lower jaw in front and behind, forbidding any but a direct movement. This is the case in the peccary, but it is not found in the hippopotamus, the *Quadrupana*, or the *Anthropoidea*. In the lophodonts, type one (mostly *Ungulata*), the mandibular condyle is not confined in front, and thus it has free lateral movement. In the second type of lophodonts (*Rodentia* and *Proboscidea*) the condyle is not confined anteriorly or poste-

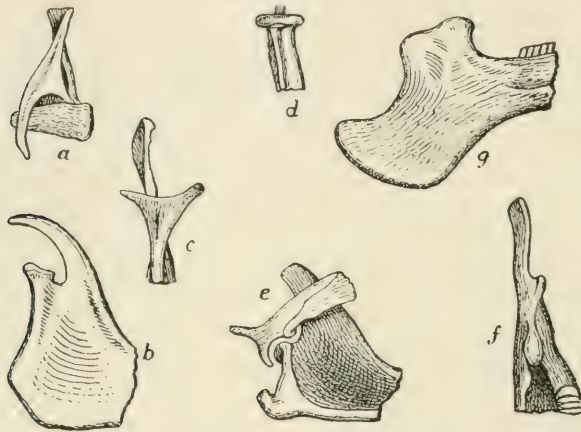


Figure 74. — Skull articulations of the mandible in *a, b, c*, the giraffe; *d, e*, wild cat; and *f, g*, *Hydrochærus*. Figs. *a* and *f*, vertical views; *b, e*, and *g*, profiles; and *c* and *d*, posterior views; from Ryder.

riorly, but is bounded by a lateral longitudinal crest of the squamosal bone. The movement must be, therefore, fore and aft, whether the mouth be much opened or not.

We may now examine the cause of the evolution of the lophodont, type one, from the simple bunodont. Both types exist within the order *Diplarthra*, and it has been already shown that the former have descended from the latter in each suborder of that order.

In the accompanying figure (75) from Ryder the movements of the lower jaw in mastication of lophodonts, are diagrammatically represented. Fig. *a* represents the movement in *Carnivora*, and in the orthal bunodonts, as the pigs. Fig. *b* shows a slight lateral movement believed by Ryder to exist in the wart hog (*Phacochoerus*). Fig. *c* represents the movement in

kangaroos, phalangers, and tapirs. In Fig. *d* a theoretical intermediate movement is represented, such as Ryder supposed to have characterized the *Anchitherium*. In *e* the usual movement among ruminants is depicted, as is seen in the deer, etc.

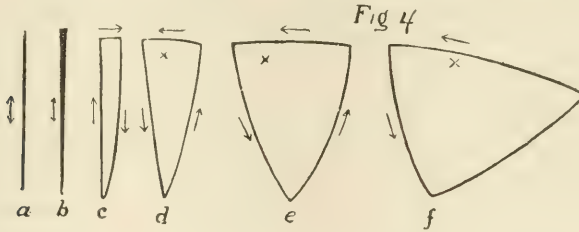


Figure 75. — Diagram of excursions of lower jaw in mastication; from Ryder.

In *f* the wider excursion of the jaw is that seen in the giraffe, camel, and ox. In these movements from *b* to *f*, the lower jaw is moved transversely across the upper jaw from one side to the other.<sup>1</sup> Some of the *Diplarthra* masticate on one side of the jaw when performing this movement, and some on the other. That is, in passing the lower jaw across the face of the upper, some masticate the food on the side where the external face of the lower jaw crosses the upper jaw from within outwards (ental); while in other types the food is masticated on the side where the lower jaw passes the external edge of the upper jaw from without inwards (ectal). While masticating with one side of the jaws, the opposing dental series of the other side are not in contact. All mutual effect of the teeth of one jaw on the other could therefore appear on the side

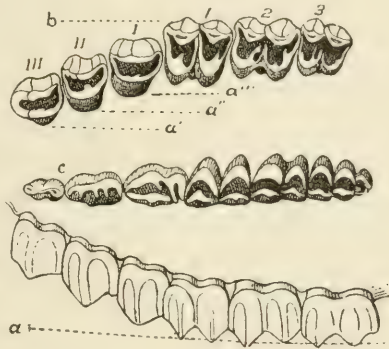


Figure 76. — *Cervus*, molars: *a*, superior, external view; *b*, do. inferior view; *c*, inferior molars, superior view; from Ryder.

<sup>1</sup> Ryder was at first of the opinion that the grinding process was produced by the movement from within outwards in all cases; *l.c.*, p. 65. He afterwards observed that the movement was the reverse in the rhinoceros, or from without inwards, and he then changed his former opinion and regarded the latter movement as universal. I have shown that both Ryder's observations are correct, and applicable to different groups.

temporarily used for mastication only. Among recent Ungulata the ruminants present the ental mastication; the rhinoceros and horses, the ectal; and rodents and proboscideans, the proal and palinal respectively.

When the crests of the inferior molars were developed, their relation to the crests of the superior molars was always anterior in mastication. That is, the inferior crest, in the closing of the jaw, collides with the crest of the upper molar, with its posterior edge against the anterior edge of the latter. This is because: *first*, as to position, the two anterior cusps of the lower molar are the remains of the anterior triangle which fit originally be-



Figure 77.—Cusps of superior premolars and molars: *a*, external cusp of molar of *Sarcothraustes*; *b*, of *Phenacodus*; *c*, of *Anthracotherium*; *d*, of *Oreodon*; *e*, half of inferior molar of *Cervus*; *f*, superior premolar of *Coryphodon*; from Ryder.

tween two superior molars, and because, in the closing of the jaw, these cusps continue to hold that position; and *second*, as to function, because the canine in the ungulate series diminishes in size, and does not, therefore, draw the inferior molars forwards as in the Carnivora, but allows free scope to the posterior traction of the temporal muscle in its exercise on the lower jaw.

In those forms which masticate from the inside outwards, the cusps of the inferior molars, passing between those of the superior molars, would tend to flatten the sides on which they exerted friction, and to extend those sides outwards beyond the median apex of the cusp. The result would be, and taking into view the yielding of the tissue to such strain, has been, to modify the shape of the cusp by pushing its side walls, so that a horizontal section of it would become successively more and more crescentic. The effect on the inferior teeth would be to produce the same result in their external cusps, but in the opposite direction. The sides of the cusps would be pushed inwards, past the apex, giving a crescentic section more or less perfect, as the operation of the cause had been of long or short duration. The

result of the lateral movement in mastication may be understood by reference to the accompanying cut. The external crescents (*c*) of the inferior molars (*b*) are seen to pass between the internal crescents (*d*) of the superior molars (*a*). The mutual interaction and effect on the form of the crescents may be readily understood. In Fig. 77 the successive stages of this effect on one or two cusps may be seen, beginning with a cone (*a*) and terminating with crescents (*ef*). Thus is the origin of the selenodont dentition of the highest Artiodactyle explained by Ryder, and, I believe, correctly.

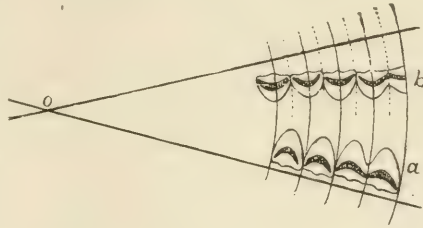


Figure 78. — Two true molars of both jaws of a ruminant: *a*, superior molars; *b*, their inner crescents; *b*, inferior molars; *c*, their external crescents; *e-f*, directions of motion of jaws in mastication; from Ryder.

The problem of the origin of the Perissodactyle types of molar dentition is somewhat different.<sup>1</sup> The peculiarity of the superior molars of Perissodactyla, as compared with Artiodactyla, is that the interior tubercles are of less elevation and complexity than the exterior. Of less importance is the fact that in the majority of forms, in the lower jaw, the internal cusps alternate with the external cusps instead of standing opposite to them as is the case in Artiodactyla. With the exception of the Tapiridæ and some Lophiodontidæ, the Perissodactyle inferior molars are amœbodont. The two arrangements are produced by different types of superior molars, but the modifications have been brought about in the same way in both antiodonts and amœbodonts.

In the Hyracotheriinae, the ancestral type of all Perissodactyla, the mandibular condyles are strongly convex, transversely as well as anteroposteriorly. The effect of this structure on mastication is to allow the ramus of the mandible to twist as it rises at the end of its transverse excursion. In other words, the contractions of the masseter and temporal muscles throw the

<sup>1</sup> Ryder has supposed, after examining the superior molars of *Symborodon*, that the modifying force has acted from without inwards, and has applied this view to all *Diplarthra*. I believe this to have been impossible, and that his first view is the correct one.



inferior molars with especial force against the external edge of the superior molars in passing or meeting them. In this way the external cusps in both jaws sustain the greater part of the strain and friction in mastication. Thus it is, I suspect, that the external cusps have acquired such pre-eminent dimensions in this order. They have also sustained the same lateral shearing from within outwards that the internal crests have experienced in the selenodont Artiodactyla, and with the same result, their gradual modification into crescents. The absence of such shearing pressure between the internal cusps has resulted in their retaining their primitive conical form to a comparatively late geological age, as is seen in all forms of the order except the genera *Hippotherium* and *Equus*.

The peculiar form of the mandibular condyle of *Hyracotherium* is visible in a less degree in *Anchitherium* and in *Symborodon*. It is still less visible in *Equus*, and is quite wanting in *Tapirus* and *Rhinocerus*. But the latter have retained the dental character inherited from the *Hyracotheriinae*.

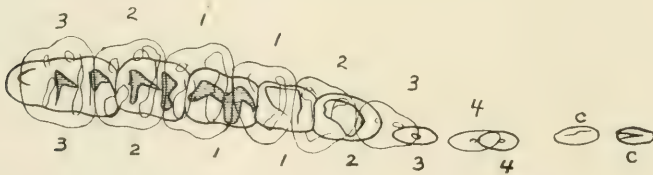


Figure 79.—*Hyracotherium venticolum* Cope; mutual relations of molars in mastication. The space bordered by light lines the superior masticating surfaces; those by heavy lines, the inferior; C, canine. Lettering as in Fig. 58.

It has been already pointed out that three lines of descent diverge from the *Hyracotheriinae*, viz.: the *Rhinocerotine*, the *Tapirine*, and the *Equine*. The origin of the dental peculiarities of these may be now considered.

In the *Hyracotheriinae* the intermediate tubercles of the superior molars, derived from the *Condylarthra*, remain, and assume an important part in the construction of the crown. In the *Artiodactyla*, on the contrary, they disappear. This is possibly due to the crowding in a transverse direction which the crowns of the molars experience in that suborder. In the *Perissodactyla* they may have one of two positions: they are either in the transverse line with the other cusps, or they alternate with

them. When they join the internal cusps and form crests, the latter are either obliquely transverse to the anteroposterior diameter of the crown (most of the genera), or directly transverse (Tapiridæ), or longitudinal (Equidæ). The causes effecting these changes may be now considered.

In the Tapiridæ the absence of any noteworthy lateral movement of the lower jaw has prevented the development of crescents on the crowns of the molars of either jaw. The fact that the intermediate tubercles of the upper jaw are opposite the external ones has led to the development of transverse crests in both jaws. The development of these crests must be regarded as the result of simple growth, which has pursued the direction of least resistance. The growth has been stimulated by the fore-and-aft mutual contact of the tubercles of each set of teeth on the other.

In the case of the genera with alternate intermediate cusps in the molars of each jaw, the connecting crests when present have naturally become oblique. We notice that from the primitive type of Hyracotheriinae, two lines possessing this character have had their origin: those of the rhinoceroses and those of the horses, the latter commencing with the Lambdotheriidæ. In the former the external crest of the superior molars do not form V's; in the latter they do (Figs. 80, 81). In both, intermediate tubercles have been developed in lines anterior to the apices of both the external and internal cusps. It results from this that when these join the inner tubercles, they form parts of crests which reach the external wall of the crown anterior to the corresponding external cusps.

As the intermediate tubercles alternate with both internal and external cusps in the upper molar, it follows that the external cusps of the inferior molars in passing from within, across the superior molars, pass obliquely over the summits of the former. This draws out the anterior external angle of the tubercle so as to form its prolongation as a crest, to the notch between the external cusps, as in *Anchitherium* (Fig. 83). When this crest is completed, the posterior oblique branch of the inferior V in vertical motion shears on its anterior edge as in other Ungulates, differing only from the tapirs in being oblique instead of transverse. In transverse horizontal motion, the lower crest crosses it at an oblique angle. In the Equine series the

posterior cingulum of the superior molar suffers attrition from the anterior crest of the anterior exterior cusp of the inferior molar. In *Anchitherium* this develops a tubercle which becomes ultimately a short crest directed outwards and backwards. This forms the third or posterior intermediate tubercle. It is wanting from the rhinoceros line. The intermediate tubercles, now crests, have the following relations to the external crests, now V's, of the inferior molar. The anterior is parallel to the posterior limb of the anterior V; the median is parallel to the posterior of the second V; the third is parallel to the anterior limb of the anterior V. The posterior forms, then, with the anterior of the tooth following it, an incomplete V, with its apex external, and therefore corresponding in direction and position to the anterior V of the inferior molar. The second inferior V is only met by a representative of its posterior branch in the upper molar. But a crest of the upper molar corresponding to its anterior branch develops later in the germs *Anchippus*. This branch first appears as a process from the median intermediate crest (Fig. 82, *iap*) extending anteriorly towards the anterior intermediate. In *Anchippus* the posterior and median intermediate tubercles unite and form a crescent opposite to the external, and connected with the posterior internal tubercle. In *Hippotherium* the anterior branch of the median joins the posterior interior extremity of the anterior median, thus forming another intermediate crescent opposite the anterior external. These intermediate crescents have exactly the same mechanical relation to the inferior crescents that the external superiors have; they alternate with them, and their horns cross obliquely in lateral mastication. We have here another illustration of the law that *the horns of molar crescents are prolonged in the direction of thrust by the corresponding parts of the opposing molar*. The interior tubercles remain small in the horse line for the reason already given, — their little use. The only exception to this rule appears at the end of the series, where in the genus *Equus* the anterior internal cusp becomes enlarged like the others.

In the rhinoceros line, where the posterior intermediate does not appear, the anterior intermediate falls into line with the transverse crest, and remains so. The median intermediate, on the other hand, develops an imperfect crescentic form in the

true genus *Rhinocerus*, after passing through intermediate stages. In the first of these it extends in a nearly straight line anteriorly, as in *Aphelops*, etc. In later genera its extremity joins a short internal process of the external wall, *e.g.* in *Rhinocerus*, but it is evident that the crescent thus formed has not the character of that which is developed in the genus *Equus*.

The essential peculiarity of the superior molars of the *Rhinocerotine* line is, that the external wall of the crown does not develop V's. This peculiarity is seen in some of the *Lophiodontine* ancestry, especially in the genus *Hyrachyus* (Leidy). Ryder has already shown that in *Rhinocerus* the mastication is ectal, but he did not apply this fact to the explanation of the

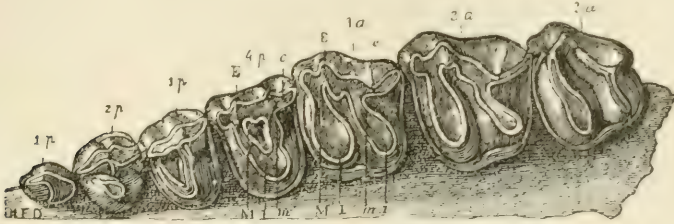


Figure 80. — *Hyrachyus agrestis* Leidy, superior molar teeth (ectal type) from below; Eocene of Wyoming; from Leidy.

absence of V's in the superior molars in this line. I suspect that the ectal mastication commenced in some of the *Lophiodontidæ*. The appearance of the anterior external cusp in *Lophiodon* and *Hyrachyus* renders this probable. In these genera the anteroposterior edges of that cusp are drawn *inwards*, as would result from the ectal mastication, and not outwards, as results from the ental (Fig. 80). It presents a narrow V, with the apex outwards. The posterior part of the external wall of the molar is, however, somewhat flexed inwards, and in some types gives the appearance of an open V directed in the opposite direction from the anterior V. This at once suggests ental mastication, and introduces the question whether the explanation offered for the origin of the anterior V is correct. Examination shows that this posterior V is not entirely homologous with the posterior V of the ental dentition, but is homologous with the entering angle between the external cusps, directed inwards instead of outwards. This is confirmed by the fact that its apex, in the Eocene genera mentioned, the point



of junction of the oblique transverse crest with the external wall, looks *inwards* instead of outwards; the true second external cusp is behind this point, as is the first external cusp in the same crown. In the inward movement of the inferior molar crown over the external wall of the superior molar in mastication, the shearing and pressure are of course effected by the posterior faces of the transverse crests of the inferior molars against the anterior faces of the corresponding crests of the superior molar. In crossing the external wall of the superior molar, the shearing is on that part which is opposite to the transverse crest, and from before backwards. The crests of the superior molars which are immediately posterior to a transverse crest receive no, or relatively little, shearing strain. The result is that the part of the wall in front of the posterior external crest and cusp is carried inwards by the ectal movement of the posterior crest of the inferior molar, while the crest behind that cusp, being without such strain, remains either in line with the anterior wall ridge, or remaining in its original position posteriorly, is carried inwards with the anterior crest and cusp, thus forming an open V. It is also probable that in this line there has been in mastication a rotary movement of the inferior molars on the superior. The ectal has evidently been a backward movement as well; if so, the ental movement would be a forward one. Such a movement would at once account for the outward flexure of the posterior free extremity of the external wall of the superior molar (Fig. 8o); since it would in that case receive the outward shear of the anterior part of the inferior molar behind and below it. The same movement would account for the external extension of the anterior cingulum of the superior molars, which is such a characteristic peculiarity of the Lophiodontidæ and of their Rhinocerontine descendants.

The inferior molars of the Perissodactyla develop from the primitive quadritubercular type in two directions, the one anti-odont, the other amœbodont, as already stated. In the former the cusps unite to form cross-crests; in the other the junction of the cusps forms a W or double crescentic pattern. We have the former in some members of the Lophiodontidæ, in the Tapiridæ, and in the Rhinocerontine series generally. The latter type is characteristic of the Equine series.

The origin of the crests is, in accordance with I. (p. 218), sim-

ple growth, resulting from use, in the direction of least resistance. Hence in teeth with opposite cusps, growth will connect them if anywhere, thus avoiding collisions with the corresponding growth in the opposite jaw. This is the primitive relation of cusps, and

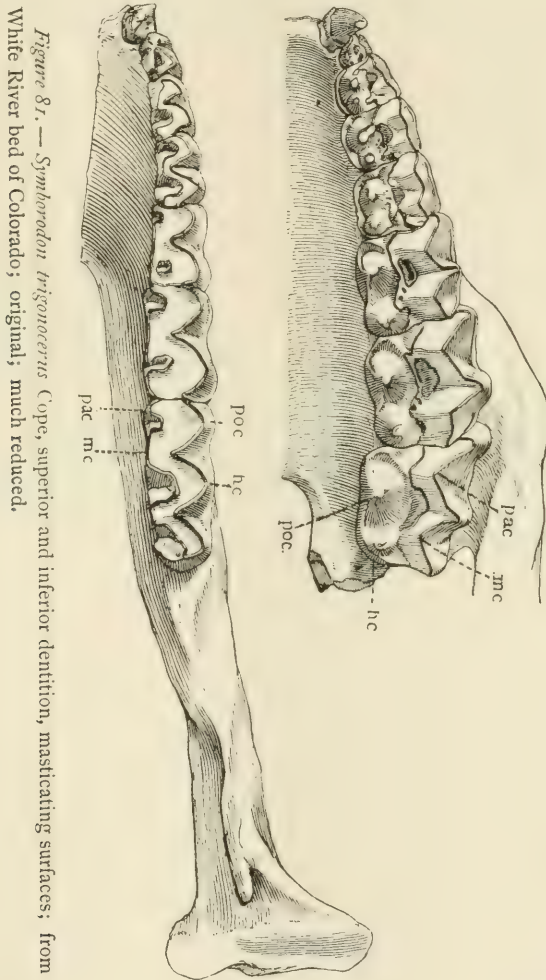


Figure 81. — *Symborodon trigonocerus* Cope, superior and inferior dentition, masticating surfaces; from White River bed of Colorado; original; much reduced.

its result. In some of the Lophiodontidæ (*e.g.* *Systemodon*) a slight alternation is observable in the cusps of the inferior molars, while those of the superior molar remain opposite. This alternation is developed to its fullest extent in *Anchitherium*, where the external and internal cusps of the superior molars are

still opposite. This peculiarity of the inferior molars is due to the development of intermediate tubercles in the superior molars, in front of the line which could connect the external and internal cusps, as has been already described. These appear in a rudimentary condition in *Hyracotherium*, and present an increasing development in all the lines of the suborder.

The mechanical effect produced by them on the opposing (inferior) molar teeth is as follows. An external cusp of the inferior molar in passing across the face of the superior molar (ental) is deflected forwards so soon as it strikes the intermediate

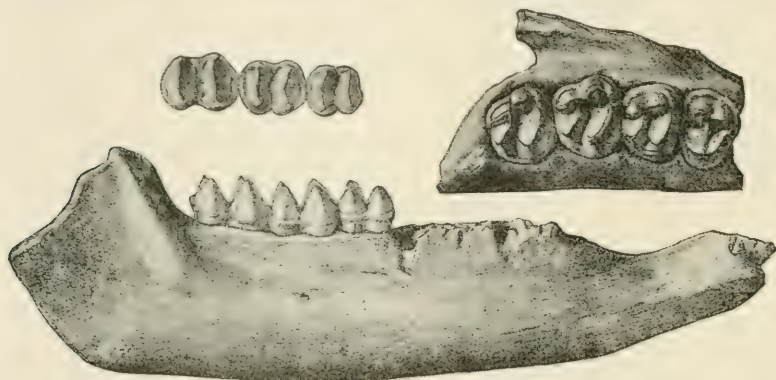


Figure 82. — *Protapirus priscus* Filhol, superior and inferior molar teeth, grinding faces; from the Eocene phosphorites of Quercy; from Filhol.

tubercle. In this position its apex is nearly opposite to the corresponding external and internal cusps of the superior molar. As the inferior molar is narrower than the superior, its interior cusps become engaged with those of the superior molar, as the external cusps of the former reach the intermediate cusps of the latter. Now were the internal cusps of inferior molar directly opposite to the external cusps of the same, the former would in these circumstances come into collision with the internal cusps of the upper series. In order to pass through the intervals of the internal cusps of the superior molars, the internal cusps of the inferior molars must alternate with the exterior cusps of the same. They have been forced into this position by the constant pressure on and by the internal cusps of the superior molar, which they engage on the posterior side, and not on the anterior side, as is the case in types where the intermediate tubercles are either in transverse line with the

others, or are wanting. The development of V's from these alternating cusps has then proceeded as in other types, with the exception peculiar to the *Perisodactyla* already referred to, that the external cusps only in both jaws are thus developed (Fig. 83).

## II. ORIGIN OF THE PROAL DENTITIONS.

*A. Rodentia.* The phylogeny of the Rodentia as an order is now tolerably clear. I at first suggested,<sup>1</sup> and later asserted<sup>2</sup> that this order was derived by descent from the Tillodont suborder of the Bunotheria. The Tillodont suborder had a common origin with the Tæniodonta, from some type of Bunotheria with unspecialized molars and premolars, in which some of the incisor teeth had begun to display enlarged size. A form allied to this ancestor is the genus *Esthonyx*, which differs from it in but few respects. Professor Ryder, in discussing the origin of the Rodentia,<sup>3</sup> writes as follows: "The significance of accessory rudimentary incisors present in some forms of true rodents, as pointing to the manner in which the evolution of the rodent type of dentition took place, may be overrated; yet when it is borne in mind that in other groups the appearance of diastemata between the different kinds of teeth took place gradually, and in

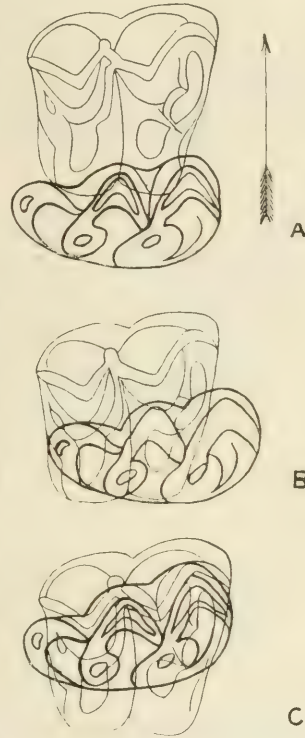


Figure 83. — *Anchitherium equiceps* Cope; superior and inferior molars in apposition, showing relations of crests at different stages of mastication; one-half larger than nat. size; original. *A*, The last inferior molar beginning its transit across the superior molar, at the inner margin. *B*, The internal cusps of the former between those of the latter. *C*, The internal of the inferior between the external of the superior.

<sup>1</sup> *American Naturalist*, April, 1883; report U. S. Geol. Surv. *Tertiary Vertebrata*, 1885, p. 814.

<sup>2</sup> *Loc. cit.*, April, 1884.

<sup>3</sup> *Proceedings Academy Philadelphia*, 1877, p. 317.



a way which unmistakably shows the gradual steps of the process, we may be excused for thinking the same to have been the case here, although without positive tangible evidence in the shape of intermediate fossil forms that exhibit such a passage from

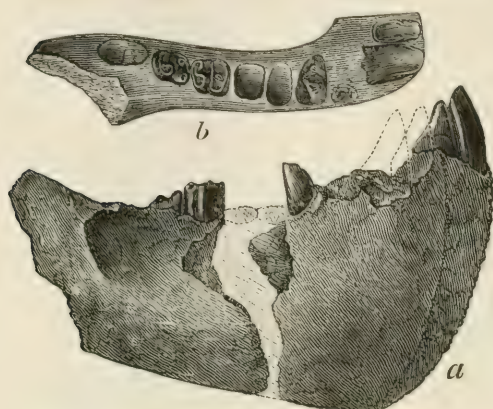


Figure 84. — *Psittacotherium multifragum* Cope, left mandibular ramus; one-half nat. size; original; from Puerco bed of New Mexico. Fig. *a*, external view; *b*, superior view.

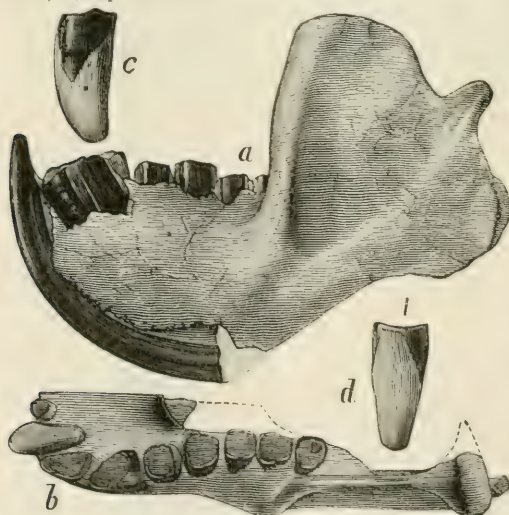


Figure 85. — *Calamodon simplex* Cope, lower jaw, left ramus; one-third nat. size; original; from Wasatch Eocene of Wyoming. Fig. *a*, external view; *b*, superior; *c-d*, inferior molar; *c*, exterior, *d*, posterior views.

the ordinary type." In 1882 I had the pleasure of discovering a genus<sup>1</sup> (*Psittacotherium* Cope), which supplies the desideratum wanting when Professor Ryder wrote. This is a genus without diastema, and with two effective rodent-like incisors in each ramus of the lower jaw. *Ectoganus* Cope is probably similar in these respects, but only its separate teeth have been found. *Psittacotherium* is then a generalized type and is not far from if not directly in the line of the ancestry of all Rodentia. It belongs to the Puerco fauna, which embraced so many of the progenitors of later Mammalia (Fig. 84).

I have called attention to the fact that the first inferior inci-

<sup>1</sup> *American Naturalist*, February 1882. *Tertiary Vertebrata*, 1885, p. 195.

sor is rudimental in Calamodon, and Marsh has shown the same thing in Tillotherium. In both genera the second incisor is the effective tooth. The third is apparently present in Calamodon (Fig. 84), but the homology of this third tooth is not yet fixed. In Tillotherium the third incisor is apparently wanting. In Psittacotherium the first incisor tooth is present and effective, but the second is larger. It is not certain whether these are first and second, or second and third incisors. If we allow Esthonyx to decide the question, the large second tooth is truly the second incisor, for in that genus the first incisor is small, and the third is rudimental. With present information, then, the inferior incisor of the Rodentia is the second of the Mammalian series.<sup>1</sup>

The peculiarities of the rodent dentition consist, as is well known, in the great development of the incisors; the loss of all but one, or rarely of two, of the premolars, which leave a wide diastema; and the posterior position of the molar teeth, as relates to the rest of the skull. A peculiarity which belongs to the highest types of the order is the prismatic form of the molars, and the deep inflection of their always transverse enamel folds both laterally and vertically. A peculiarity of the masticating apparatus, which is the basis of distinction from the Bunotherian order, is the lack of postglenoid process, and the consequent freedom of the lower jaw to slide backwards and forwards in mastication. Appropriately to this motion the condyle of the mandible is either subglobular, or is extended anteroposteriorly, and the glenoid cavity is a longitudinal instead of a transverse groove.

The mechanical action of the development of the rodent dentition has been as follows. The first factor in the order of time and importance was the increasing length of the incisor teeth. Those of the lower jaw closed behind those of the upper in the progenitors of the Rodentia (*e.g.* Esthonyx) as in other Mammalia. Increase of length of these teeth in both jaws

<sup>1</sup> I have regarded (*Naturalist*, 1884, April and earlier) the Tæniodonta as the ancestors of the Edentata. The objection to this view is the supposed absence of inferior incisors in the latter. But the middle incisors have disappeared from some of the Tæniodonta, while the supposed canines of the lower jaw of Megalonyx and allies may be true incisors. This is rendered probable by the genus *Diadomus* of Ameghino, where the large canine-like teeth are close together at the symphysis mandibuli, like the incisors of the Tæniodonta and Rodentia.

would tend to keep the mouth permanently open, were it not for the possibility of slipping the lower jaw backwards as it closed on the upper. This backward pressure had undoubtedly existed, and has operated from the earliest beginning of the growth of the rodent incisors. The process has been precisely the opposite of that which has occurred to the Carnivora, where the pressure has been ever forwards owing to the development of the canines.<sup>1</sup> The progressive lengthening of the incisors through use has been dwelt on by Professor Ryder (*l.c.*). The

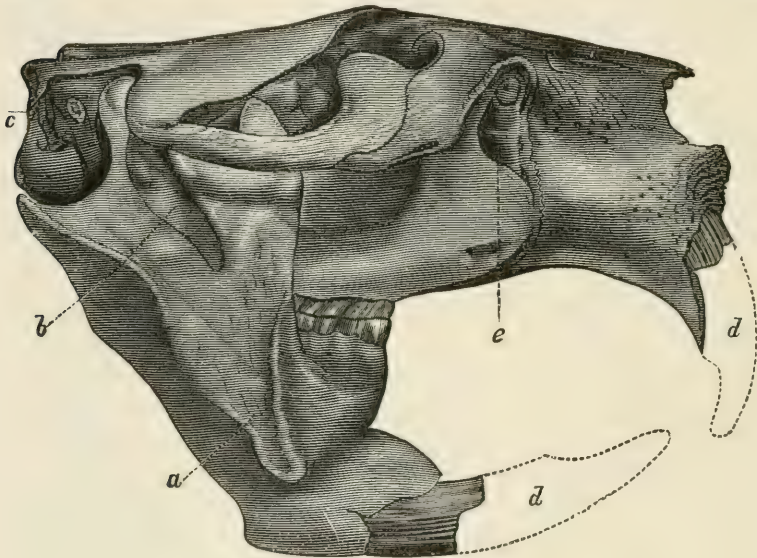


Figure 86. — *Castoroides ohioensis* Foster, skull, right side; two-fifths nat. size. Fig. *a*, inferior insertion of masseter muscle; *b*, fossa inside of ascending ramus; *c*, external auditory meatus; *d*, incisors; *e*, foramen infraorbitale; from Hall and Wyman.

posterior pressure on the lower jaw produced by its closing on the upper, has been increased directly as the increase in the length of the incisors, especially those of the lower jaw.

The first effect of this posterior pressure will have been to slide the condyle of the mandible posteriorly over the postglenoid process, if any were present, as is probable, in the Bunotherian ancestor of the rodent. Continued repetition of the movement would probably push the process backwards so as to render it ineffective as a line of resistance, and ultimately

<sup>1</sup> Antea, p. 232.



to flatten it out against the otic bulla, and atrophy it. The lower jaw would thus come to occupy that peculiarly posterior position which it does in all rodents.

The anteroposterior (proal<sup>1</sup>) type of mastication becoming necessary, an appropriate development of the muscles moving the lower jaw, with their insertions, follows, *pari passu*. As a result we see that the insertion of the temporal muscle creeps forward on the ramus, until in the highest rodents (*Cavia*) it extends along the ramus to opposite the first true molars. The office of this muscle is to draw the ramus backwards and upwards, a movement which is commenced so soon as the inferior incisor strikes the apex of the superior incisor on the posterior side. By this muscle the inferior molars are drawn posteriorly and in close apposition to the superior molars. Connected with this movement, probably as an effect, we find the coronoid process of the mandible to have become gradually reduced in size to complete disappearance in some of the genera, *e.g.* of Leporidæ. In these genera the groove-like insertion of the temporal muscle develops as the coronoid process disappears.

As third and fourth effects of the posterior position of the lower jaw, we have the development of the internal pterygoid and masseter muscles and their insertions and origins. The angle of the ramus being forced backwards, these muscles are gradually stretched backwards at their insertions, and their contraction becomes more anteroposterior in direction than before. The internal pterygoid becomes especially developed, and its point of origin, the pterygoid fossa, becomes much enlarged. The border of the angle of the mandible becomes more or less inflected. In their effect on the movements of the ramus they oppose that of the temporal muscle, since they draw the ramus forwards. They are the effective muscles in the use of the incisor teeth; that is, in the opposition of the inferior incisors against the superior from below and posteriorly. Hence the great development of the internal pterygoid and, in a less degree, of the masseter. Both muscles tend also to close the jaws, but at a different point in the act of mastication from that at which the temporal acts. If we suppose the mouth to be open, the action of the masseter and internal pterygoid muscles draws the mandible forwards and upwards until the incisors have performed

<sup>1</sup> See page 226 for explanation of the different modes of mastication.



their office, or the molars are in contact with each other or with the food. They then relax, and their temporal muscle continues

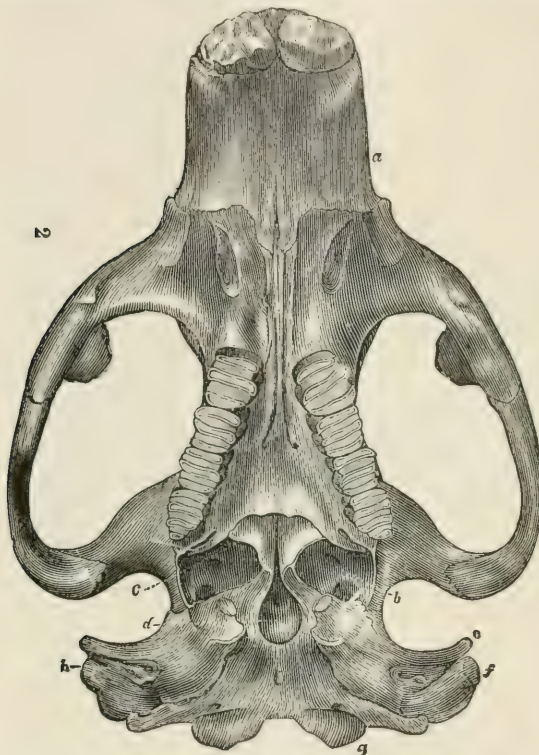


Figure 87. — *Castoroides ohioensis* Foster; two-fifths nat. size; skull from below. Fig. *a*, incisive foramen; *b*, pterygoid fossa; *c*, internal pterygoid plates; *d*, fossa in basioccipital bone; *e*, external auditory meatus; *f*, mastoid process; *g*, occipital condyles; *h*, tympania bulla; after Hall and Wyman.

the upward pressure, but draws the ramus backwards to the limit set by the adjacent parts, causing the act of mastication.

A fifth effect of the development of the incisors and of the proal mastication, is seen in the position of the molar teeth. The indefinitely repeated strain and pressure applied to the superior molars from forwards and below has evidently caused a gradual extension of the maxillary bone backwards, so that the last molars occupy a position much posterior to that which they

do in other orders of Mammals. This is especially the case in such forms as *Bathyergus*, *Arvicola*, and *Castoroides* (Fig. 86), where the last molars are below the temporal fossa, and posterior to the orbit.

A sixth effect of the causes mentioned has been referred to by Ryder.<sup>1</sup> This is the oblique direction of the axes of the molar teeth. These directions are opposite in the two jaws; upwards and forwards for the lower, and downwards and backwards for the upper. The mechanics of this change of direction

<sup>1</sup> *Proceedings Academy Philadelphia*, p. 66, Figs. 8, *b* and *f*.

from vertical in the primitive forms (*Sciuridæ*) to oblique in the genera with prismatic molars, is simple enough. The inferior crowns when closely appressed to the superior, and drawn posteriorly in the direction of the long axis of the jaw, press and strain the teeth in the two directions mentioned. The development of the long prismatic crowns which has proceeded under these circumstances, has been undoubtedly affected by the pressure and strain, and the direction we find has been the result.

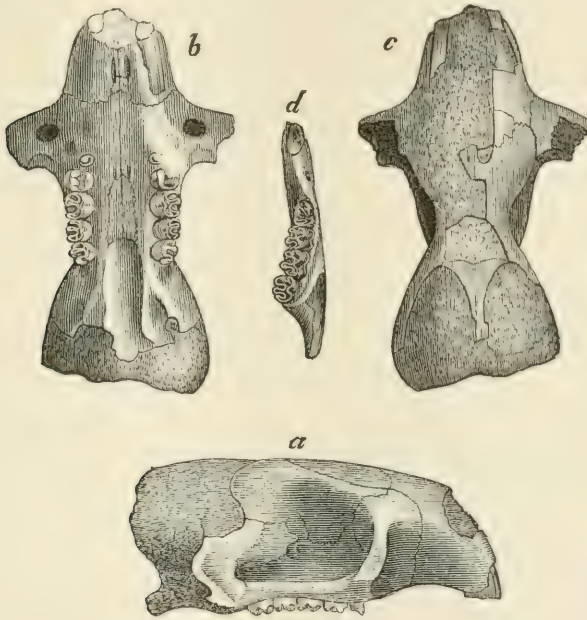


Figure 88. — *Ischyromys typus* Leidy, from the White River beds of Colorado; original; from the Report U. S. Geol. Surv. Terrs.: *a*, *b*, *c*, cranium; *d*, mandible from above.

The seventh effect is in the detailed structure of the teeth themselves. Beginning with short crowns with simple transverse crests (*Psittacotherium* and *Sciuridæ*, Figs. 84, 88), we reach through intermediate forms, crowns with vertical laminæ of enamel, which sometimes divide the crown entirely across (*Chinchillidæ*, *Caviidæ*, *Castoroididæ*) or appear only on the side of the crown, through the continued coalescence of the prisms of which each molar crown is composed (*Arvicola*). In many instances the crowns increase in transverse at the expense of

their longitudinal diameter (Castor, Lepus). The vertically laminated structure is evidently due to the crowding together of

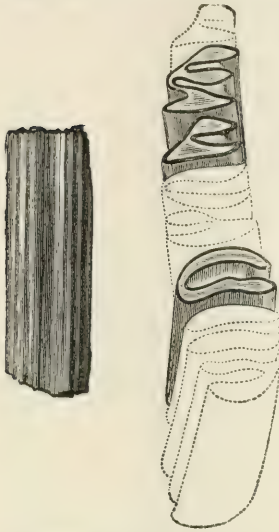


Figure 89. — Teeth of *Hydrochærus asopi* Leidy; nat. size; from Charleston, S. C.; after Leidy: *a*, fragment of superior incisor; *b*, the shaded portions represent parts of inferior molars found.

transverse crests by the same pressure which has given the crowns their oblique direction. In many genera the lengthening of the crown has included the lengthening of the longitudinal connection between the transverse crests, as in *Arvicola*, *Castor*, and *Hystrioidæ* generally. In others this connection has not been continued, so that the crown is composed of prisms which are separate to near the base, as in *Amblyrhiza* and *Saccomyidæ*. In others, connection between the prisms has been lost by cœnogeny, as in *Chinchillidæ* and *Caviidæ* generally. The latter families display also the greatest amount of crowding (Fig. 89).

A peculiarity of the plication of rodent molars I am unable to explain as yet on mechanical principles. In genera which are isognathous, the inflections are of equal depth on opposite sides of both superior and inferior molars. In anisognathous genera the inflections are more numerous and profound on opposite sides of the molars of the respective jaws. Anisognathism in rodents is generally as shown by Ryder, of the type where the

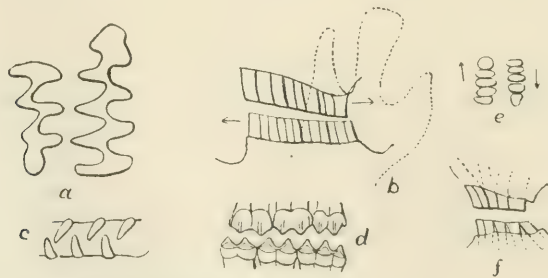


Figure 90. — Molars of Rodentia compared with the haplodont (*a*) and selenodont (*d*) dentitions: *a*, *Arvicola*, first inferior molars; *b*, do. profile; *c*, *Thomomys* crowns; *f*, do. profile; from Ryder.

inferior molars include a wider expanse than the superior, though this applies in some instances more to the direction of the roots rather than the position of the crowns. In *Lepus* the lower jaw is the narrower. I have termed the two types of anisognathism hypanisognathism (*Lepus*, *Diplarthra*) and epanisognathism (*Caviidæ*). The following genera display these characters:—

*Hypanisognathous.*

*Lepus.*

*Isognathous.*

*Arvicola.*

*Capromys.*

*Epanisognathous.*

*Hystrioidæ.*

*Castor.*

*Caviidæ.*

In conclusion I will say that it is satisfactorily proven to my mind that nearly all of the peculiarities of the rodent dental system and manner of mastication, are the mechanical consequences of an increase in the length of the incisor teeth. And the increase of the length of these teeth has been due to their continued use, as believed by Ryder.

*b. Monotremata Multituberculata.* The structure of the dentition of this suborder is in many respects like that of the Rodentia in the known forms. The incisors in the *Plagiaulacidæ*, *Chirogidae*, and *Polymastodontidæ* have structure and functions generally similar to those of the Rodentia. The result in the form and function of the molar dentition has been similar to that observed in the Rodentia. The postglenoid process is probably absent in these animals; in any case the mandibular condyle is rounded, and is not transverse. Prof. H. F. Osborn has pointed out to me that mastication was performed by a fore-and-aft movement of the inferior molars on the superior in *Plagiaulacidæ*. This was no doubt the case in the other families named. The resulting structure of the crown is, however, different, and needs explanation. The molar teeth present conical

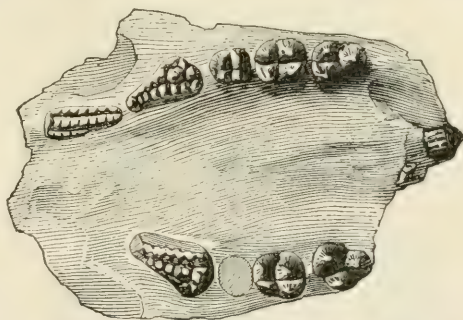


Figure 91. — *Chirox plicatus* Cope, palate and molar teeth from below; three-halves nat. size; from Puerco bed of New Mexico; from American Naturalist, 1887, p. 566.



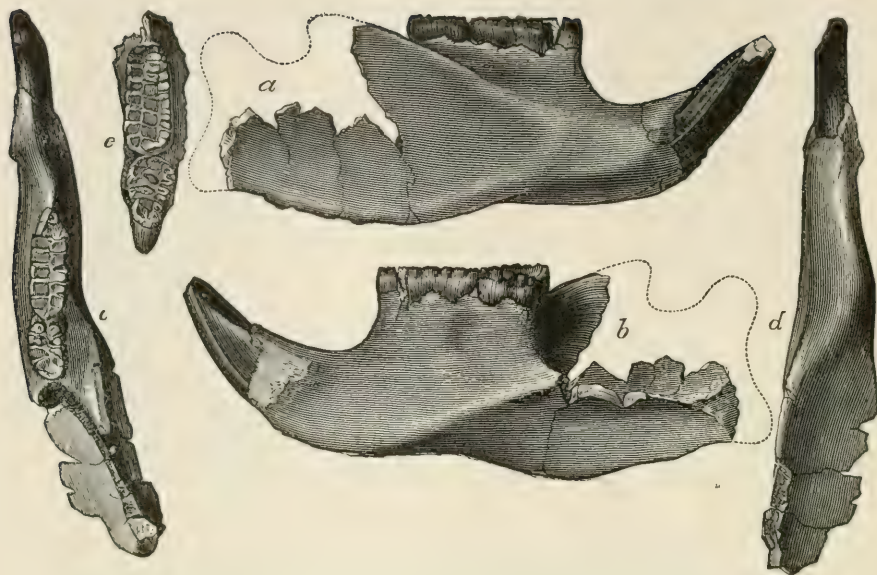


Figure 92.—*Polymastodon taënsis* Cope, jaws two-thirds nat. size; from Puerco bed of New Mexico. Figs. *a*, *d*, lower jaw; *c*, upper jaw; original.

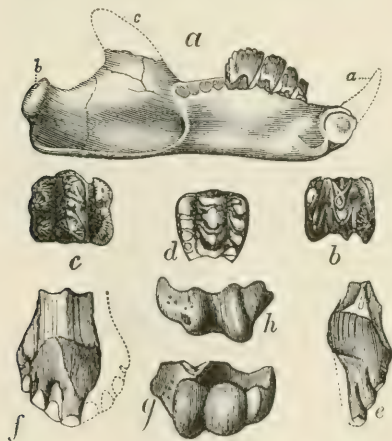


Figure 93.—Monotremata Multituberculata. Fig. *a*, *Clenacodon serratus* Marsh; three times nat. size; from Marsh; *d*, *f*, *Meniscoessus conquistus* Cope, three halves nat. size: *d*, superior molar; *g*, humeral condyles; *h*? premolar. Fig. *b*, *Stereognathus obliticus* Owen; three times nat. size; from Owen; *c*, *Tritylodon longævus* Owen; three times nat. size; from Owen.

tubercles in longitudinal series, two in the lower and three in the upper jaw. The two series of the lower jaw alternate with the three in the upper jaw, moving in the grooves between the latter, while the three series of the upper molars reciprocally embrace the two of the lower molars. This is demonstrated by the mutual wear of the tubercles seen in *Ptilodus* and *Chirox* (Fig. 91). The trituration was probably the same in *Tritylodon*, but in *Polymastodon* the increased thickening of the tubercles prevented their interlocking action in mastication. In this

genus the tubercles slid over each other, and truncated the apices until in old specimens they were entirely worn away (Fig. 92, *c*, *e*). In *Meniscoëssus* and *Stereognathus* we have an interesting illustration of the effect of the action of cusps on each other when under prolonged mutual lateral thrust. Their external sides have been drawn out into long angles in the direction of thrust, converting their transverse sections from circles to crescents. As the thrust is in the *Multituberculata* longitudinal, the crescents are transverse to the axis of the jaw. In the selenodont *Diplarthra*, where the thrust is transverse to the line of the jaw, the crescents are longitudinal. That similar effects should accompany similar movements in two groups of *Mammalia* so widely separated as these two is strong evidence in favor of the belief that the two facts stand in the relation of cause and effect (Fig. 93, Figs. *b* and *d*).

#### IV. CONCLUSIONS.

Summarizing the preceding investigations, the structure of the Mammalian skeleton and dentition may be referred broadly to the two general classes: excess of growth, and defect of growth. Each of these may be again divided into two series, as follows:—

Excess of growth,	{	Use.
		Luxuriance.
Defect of growth,	{	Disuse.
		Poverty.

Progressive evolution results principally from the first two conditions, which have frequently coöperated in the development of structures. These may be classified as effects of the following mechanical causes:—

##### A. Motion in Articulation.

##### 1. Impact only, or chiefly.

Facetting of distal end of radius in *Diplarthra*.

Expansion of proximal end of radius in *Diplarthra*.

External trochlea of metapodials in *Diplarthra*.

Grooving of distal end of tibia by astragalus.

Grooving of proximal end of astragalus by tibia.

## 2. Torsion only.

Alternation of carpal bones in Anthropomorpha.  
Rounding of head of radius in Edentata and Anthropomorpha.  
Symmetrical flanges of ulnar cotylus in Anthropomorpha.  
Unsymmetrical flanges of ulnar cotylus in most Mammalia.  
Involution and sculpture of zygapophyses of Diplarthra.

## 3. Torsion and impact without flexure.

Alternation of carpal and tarsal bones in Ungulata.

## 4. Torsion, impact and flexure in one plane.

Tongue-and-groove joint in humerus of Diplarthra.  
Tongue-and-groove joint in metapodials of all orders.  
Tongue-and-groove joint in phalanges of Edentata, Insectivora,  
etc.

## 5. Flexure in two planes.

Saddle-shaped cervical vertebræ in Quadrumana.

## 6. Flexure in several directions.

Ball-and-socket vertebral articulations.  
Head of humerus.  
Head of femur.

## AA. Motion not in Articulation (Teeth).

## 7. Displacement by crowding.

Tritubercular molars.

## 8. Transverse thrust.

The V's in molars of both jaws in various orders.

## 9. Longitudinal thrust.

The V's in the molar teeth of the Multituberculata.  
Obliquity of molars in many Rodentia.

## 10. Stimulation of pressure and strain.

Prismatic molars of Diplarthra, Rodentia, etc.  
Sectorial teeth of Carnivora.

Confluence of cusps into crests generally.

Canine teeth in general.

Incisors of Rodentia, Multituberculata, etc.

Incisors of Proboscidea, of Monodon, Halicore, etc.

The relation of stimulus to nutrition is as yet so little understood, that there is plausible ground for the assertion that the hypothesis that use develops structure is "not proven." What evidence there is, however, mostly supports the hypothesis, but the proof of the theory of kinetogenesis (*i.e.* the origin and development of structure through motion) is not in the least indefinite or inconclusive. I point especially to the history of the articulations, as described in the preceding pages. And the general principles which we derive from the investigation are applicable to the entire animal kingdom.

The general law which we may derive from the preceding evidence is, that in biological growth, as in ordinary mechanics, *Identical causes produce identical results.* The evidence may be arranged under two heads, viz. :—

I. The same structure appears in distinct phyla which are subjected to the same mechanical conditions. Examples: the identical character of the articulations of the limbs in Diplarthra and Rodentia which possess powers of rapid locomotion. The identical structure of the head of the radius in Edentata and Quadrumana which possess the power of supination of the manus. Identical reduction of the number of the digits under increased use of the limbs in many of the orders. Identical modifications of the form and development of the crests of the skull under identical conditions of use of the canine teeth for defence in all the orders where the latter are developed. Identical modification of dental cusps into longitudinal V's and crescents under transverse thrusts in several orders, and into transverse crescents under longitudinal thrusts in Multituberculata.

II. Different structures appear in different parts of the skeleton of the same individual animal, in direct correspondence with the different mechanical conditions to which these parts have been subjected. Examples: the diverse modifications of the articulations of the limbs in consequence of the uses to which they have been put, in mammals which excavate the earth with one pair of limbs only; as in the fossorial Edentata,



Insectivora, and Rodentia. The reduction of the number of the digits in the posterior limb only when this is extensively used for rapid progression, as in leaping; this is seen in the kangaroo and jerboas, in the orders Marsupialia and Rodentia.<sup>1</sup>

There are a good many structures in the skeleton of the Mammalia which have not yet received a satisfactory explanation on the ground of mechanical necessity. Such, for instance, appears to me to be the history of the origin of the canine tooth; that is, its use in preference to an incisor for raptorial purposes. Such may be also the history of the origin of the complex vertebral articulations of the American Edentata as compared with the simple articulations of those of the Old World. In these as in similar cases, however, an element enters which must be taken into account in seeking for explanations; that is, that every evolution is determined at its inception by the material or type from which it originates. Thus is explained the fact that identical uses have not produced identical structures in the limbs of all aquatic vertebrates. The fin of the fish is essentially different from the paddle of the Ichthyosaurus or the whale. The beak of the raptorial bird is different from the canine tooth of the rapacious mammal. When this principle is duly considered, many mechanical explanations will become clear which now seem to be involved in difficulty or mystery.

## V. LITERATURE.

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1888. Ryder, J. A. The several functions of the enamel organ in the development of the teeth of mammals, and on the inheritance of mutilations. American Naturalist, p. 547.
1889. Cope, E. D. American Naturalist, March; The Artiodactyla. (The elbow joint; the zygapophyses.)

## VI. LIST OF CUTS IN THE TEXT.

- FIG. 1. Limbs of *Phenacodus primævus* and *Homo sapiens*.
- FIG. 2. Posterior limbs of Artiodactyla: A, *Merycocharus montanus*; B, *Bos taurus*.
- FIG. 3. *Tarsius spectrum*, posterior limb; from De Blainville.
- FIG. 4. Tarsi of bats; from Allen.
- FIG. 5. Anterior limb of right whale; from Cuvier.
- FIG. 6. *Putorius vison*, muscles of the posterior leg; original diagram.
- FIG. 7. *Monachus albiventer*, fore and hind limbs; original.
- FIG. 8. *Pantolambda bathmodon*, posterior digit; original. *Coryphodon elephantopus*, posterior foot; original. *Uintatherium mirabile*, posterior foot; from Marsh.
- FIG. 9. *Phenacodus primævus*, anterior foot; original.
- FIG. 10. *Hyracotherium venticolum*, anterior foot; original.
- FIG. 11. *Protophippus sejunctus*, posterior foot; original.
- FIG. 12. *Pœebrotherium labiatum*, fore and hind feet; original.
- FIG. 13. *Equus caballus*, fore and hind feet; from Cuvier.
- FIG. 14. Artiodactyla, fore feet; from Kowalevsky.
- FIG. 15. *Procyon lotor*, three views in locomotion, showing gait; from Allen.
- FIG. 16. *Ovis* (*Gazella*) *dorcas*; from Standard Natural History.
- FIG. 17. *Boëchærus humerosus*, distal extremity of radius and humerus, and fore foot; original.

FIG. 18. *Phenacodus primævus*, anterior foot; original. *Coryphodon* *sp.*, anterior foot; original. *Hyrracotherium venticolum*, anterior foot; original.

FIG. 19. *Smilodon neogæus*, skeleton from Buenos Ayres; from Burmeister.

FIG. 20. *Hyæna striata*; from the Standard Natural History.

FIG. 21. *Phenacodus primævus*, carpus and tarsus; original.

FIG. 22. *Hyrracotherium venticolum*, posterior foot; original.

FIG. 23. *Cervus canadensis*, from behind, trotting; from Maybridge.

FIG. 24. Anterior extremity of a bat; from Huxley and Hawkins.

FIG. 25. *Bradypus tridactylus*, posterior foot; from Cuvier.

FIG. 26. *Cholæpus hoffmanii*, three positions in locomotion; from Allen.

FIG. 27. *Coryphodon elephantopus*, posterior foot; original.

FIG. 28. *Aphelops megalodus*, posterior foot; original.

FIG. 29. *Amblyctonus sinosus*, distal end of tibia; original.

FIG. 30. *Oxyæna morsitans*, distal end of tibia; original.

FIG. 31. *Archælurus debilis*, distal end of tibia; original.

FIG. 32. *Nimravus gomphodus*, femur; original.

FIG. 33. *Pœbrotherium labiatum*, hind foot; original.

FIG. 34. *Protohippus sejunctus*, hind foot; original.

FIG. 35. *Cosoryx furcatus*, posterior cannon bone; original.

FIG. 36. *Procamelus occidentalis*, anterior foot; original.

FIG. 37. *Cosoryx furcatus*, posterior cannon bone; original.

FIG. 38. *Pœbrotherium labiatum*, anterior foot, part; original.

FIG. 39. *Manis indica*, fore foot; from Cuvier.

FIG. 40. *Priodontes maximus*, fore foot; from Cuvier.

FIG. 41. *Priodontes maximus*, hind foot; original.

FIG. 42. *Cervus elaphus*, humero-radial, and metacarpo-phalangeal articulations; original.

FIG. 43. 1, 2, *Cosoryx necatus*; 1 without, and 2 with, burr on antler. 3, 4, *Cosoryx ramosus*; 3, antler broken and reunited, 4, beam with burr; original.

FIG. 44. *Cynocephalus*, cervical vertebra, three views; original.

FIG. 45. Diagrams representing different types of locomotion, showing motion of vertebral column in each.

FIG. 46. *Cervus canadensis* in motion, from behind; showing position of legs in trot; from Muybridge.

FIG. 47. *Nimravus gomphodus*, skull; original.

FIG. 48. *Esthonyx burmeisteri*, dentition; original.

FIG. 49. *Psittacotherium multifragum*, lower jaw; original.

FIG. 50. *Lemur collaris*, dentition; original.

FIG. 51. *Triconodon ferox*, inferior dentition; from Marsh.

FIG. 52. *Menacodon rarus*, inferior dentition; from Marsh.

FIG. 53. Diagrams representing: A, relations of superior and inferior molars of *Triconodon*; B, of an intermediate type; C, ditto of *Spalacotherium*; original.

FIG. 54. *Deltatherium fundamini*, cranium and dentition; original.

FIG. 55. *Mesozoic Mammalia*, molar teeth; from Osborn.

FIG. 56. *Centetes caudatus*, dentition; original.

FIG. 57. *Lemur collaris*, profile of closed dentition; original.

FIG. 58. *Stypolophus whitia*, profile of closed dentition; superior molars superposed on inferiors, the latter in black, the former in double white outlines; original.

FIG. 59. *Cynodictis geismarianus*, skull one-half natural size; original.

FIG. 60. *Aelurodon sævus*, superior and inferior molars in relation, diagram; original.

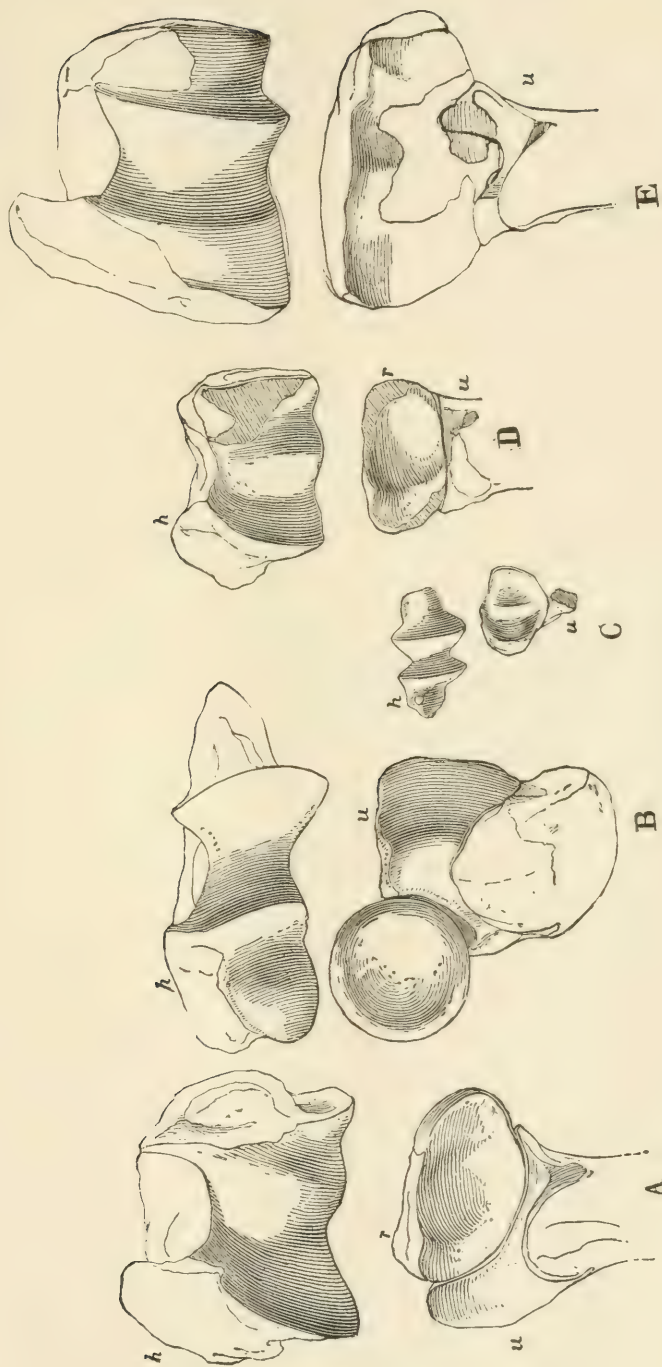
- FIG. 61. *Smilodon neogæus*, skull; original.
- FIG. 62. *Pantolambda bathmodon*, superior molars, <sup>1</sup>vertebræ, and bones of hind foot; original.
- FIG. 63. *Ectacodon cinctus* and *Metaloophodon testis*, superior molars; original.
- FIG. 64. Molars of *Coryphodontidæ* in relation, diagram; original.
- FIG. 65. *Coryphodon latidens*, mandible; original.
- FIG. 66. *Uintatherium leidianum*, molars; from Osborn.
- FIG. 67. *Uintatherium*, lower jaw; from Osborn.
- FIG. 68. *Phenacodus primævus*, diagram of molars in relation; original.
- FIG. 69. Molars of *Mammalia* in functional relation; from Osborn.
- FIG. 70. Quadritubercular and quinquetubercular molars in relation; from Osborn.
- FIG. 71. Transverse sections of molars of *Artiodactyla*; from Gaudry.
- FIG. 72. Transverse sections of molars of *Proboscidea*; from Gaudry.
- FIG. 73. Transverse sections of jaws of *Rodentia*; from Ryder.
- FIG. 74. Posterior parts of lower jaws; from Ryder.
- FIG. 75. Paths of lower jaws in mastication; from Ryder.
- FIG. 76. Dentition of *Cervus*; from Ryder.
- FIG. 77. Premolar teeth, different types; from Ryder.
- FIG. 78. Selenodont molars, both jaws, mutual relation; from Ryder.
- FIG. 79. *Hyracotherium venticolum*, molars of both jaws, mutual relation; original.
- FIG. 80. *Hyrachyus agrestis*, superior molars from below; from Leidy.
- FIG. 81. *Symborodon trigonocerus*, molars; original.
- FIG. 82. *Protapirus priscus*, molars; from Filhol.
- FIG. 83. *Anchitherium equiceps*, molars, mutual relations; original.
- FIG. 84. *Psittacotherium multifragum*, lower jaw; original.
- FIG. 85. *Calamodon simplex*, lower jaw; original.
- FIG. 86. *Castoroïdes ohioensis*, skull; from Hall and Wyman.
- FIG. 87. *Castoroïdes ohioensis*, skull from below; from Hall and Wyman.
- FIG. 88. *Ischyromys typus* Leidy, skull; original.
- FIG. 89. *Hydrochærus æsopi* Leidy, molar tooth; from Leidy.
- FIG. 90. Molars of *Rodentia*, *Delphinus*, and *Cervus*; from Ryder.
- FIG. 91. *Chirox plicatus*, superior molars; original.
- FIG. 92. *Polymastodon taoënsis*, molars and lower jaw; original.
- FIG. 93. *Multituberculata*, dentition; original.



## EXPLANATION OF PLATE IX.

*Elbow joint of Mammalia, dislocated and viewed from behind.*

- FIG. A. *Crocota maculata*.
- FIG. B. *Simia nigra*.
- FIG. C. *Rhinolophus*.
- FIG. D. *Eucrotophus pacificus*.
- FIG. E. *Cervus elaphus*.



ELBOW JOINTS OF MAMMALIA.

## EXPLANATION OF PLATE X.

*Longitudinal sections of limbs, displaying the intimate structure of the articulations.*

- FIG. 1. *Elephas africanus*, distal end of humerus.
- FIG. 2. *Elephas africanus*, tibio-astragalar joint.
- FIG. 3. *Elephas africanus*, metapodial.
- FIG. 4. *Elephas africanus*, metapodial.
- FIG. 5. *Tapirus americanus*, anterior leg.
- FIG. 6. *Ovis aries*, anterior leg.
- FIG. 7. *Ovis aries*, posterior leg.









1-4 *Elephas africanus*. 5 *Tapirus terrestris*.  
6-7 *Ovis arles*.



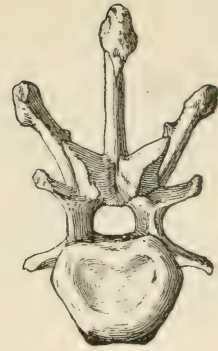
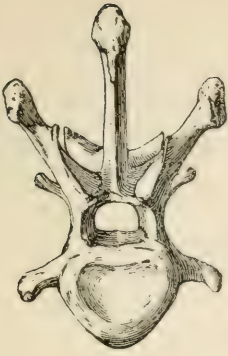




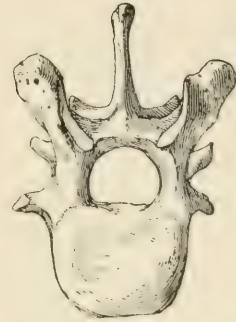
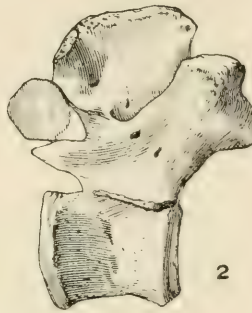
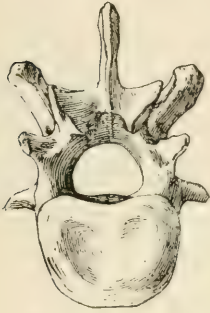
## EXPLANATION OF PLATE XI.

*Vertebra, usually the second lumbar, less than natural size.*

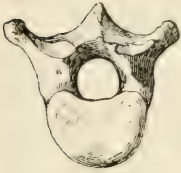
- FIG. 1. *Macropus rufus*.  
FIG. 2. *Sarcophilus ursinus*, enlarged.  
FIG. 3. *Tachyglossus hystrix*, enlarged.  
FIG. 4. *Myrmecophaga jubata*.  
FIG. 5. *Priodontes maximus*.



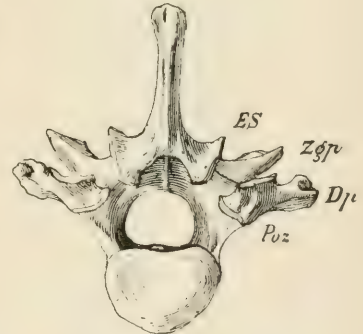
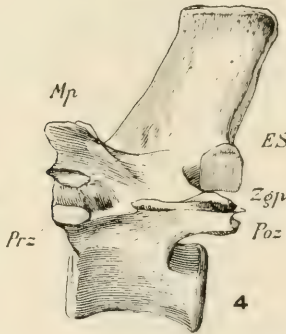
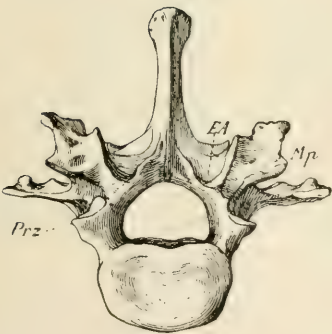
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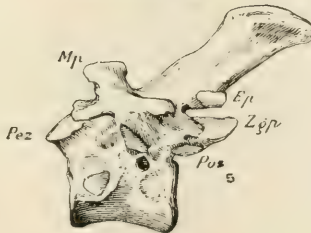
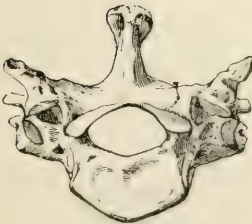
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## EXPLANATION OF PLATE XII.

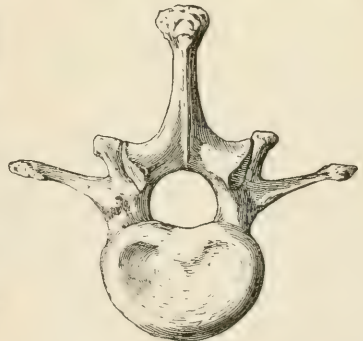
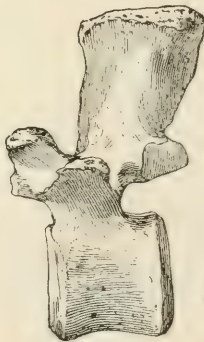
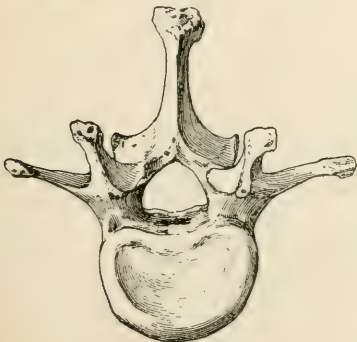
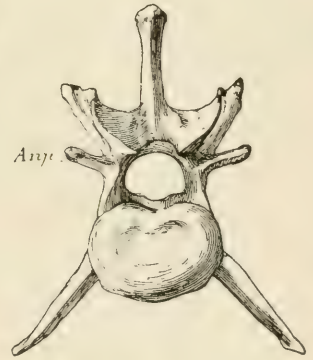
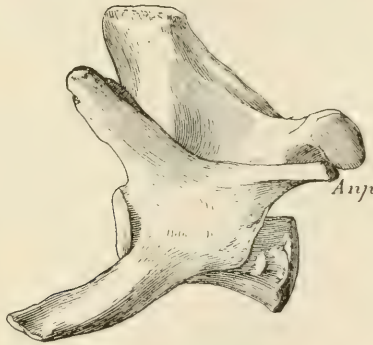
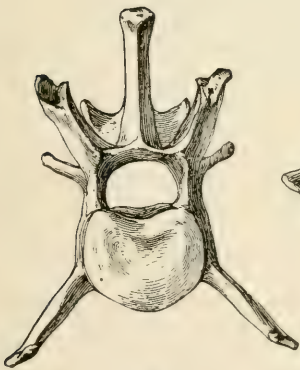
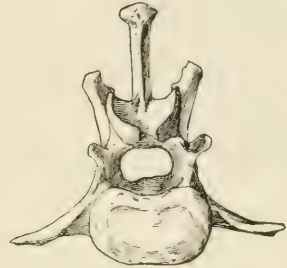
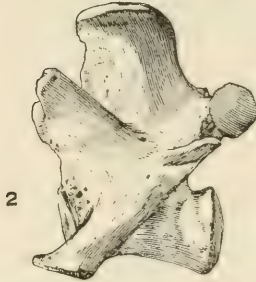
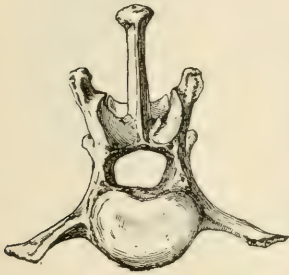
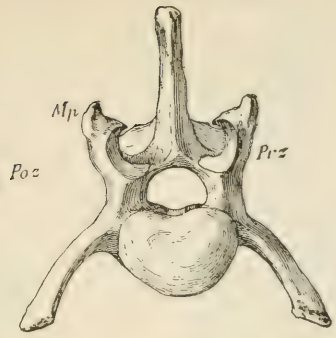
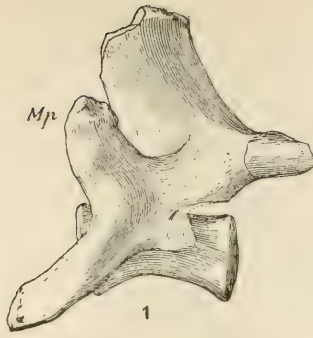
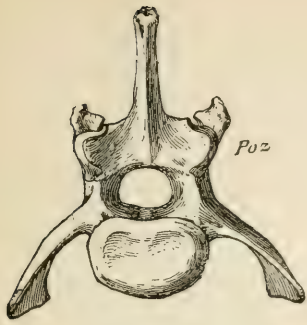
*Vertebrae, as in Plate XI.*

FIG. 1. *Mesonyx obtusidens*, from specimen in Mus., Princeton College.

FIG. 2. *Canis lupus*.

FIG. 3. *Uncia concolor*.

FIG. 4. *Simia nigra*.



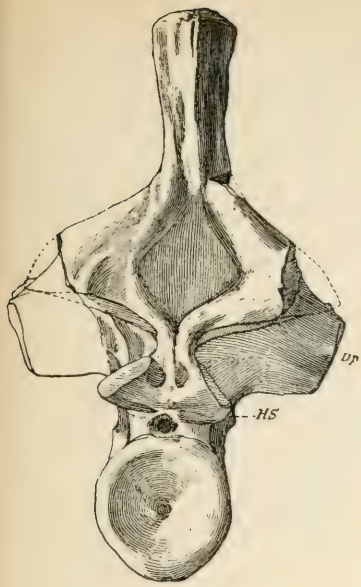


## EXPLANATION OF PLATE XIII.

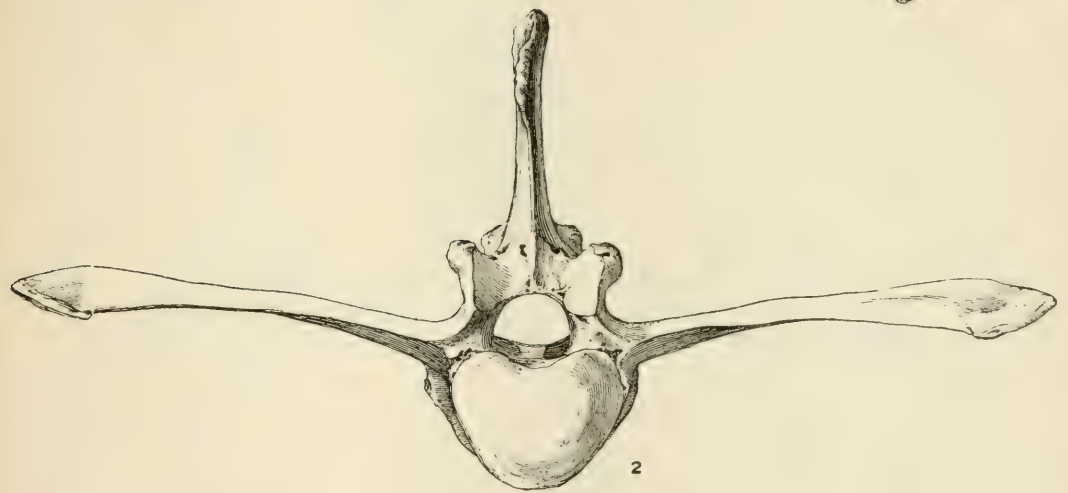
*Vertebrae, as in Plate XI.*

FIGS. 1-3. *Equus caballus*.

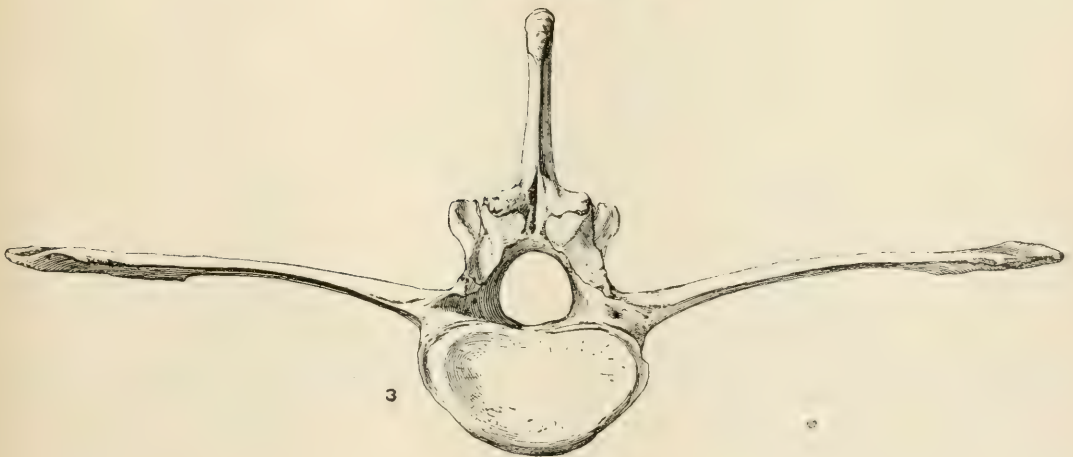
FIGS. 4-5. *Empedias phaseolinus*, showing hyposphen; a Theromorous reptile from the Permian formation of Texas.



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VERTEBRÆ.

## EXPLANATION OF PLATE XIV.

*Vertebrae, as in Plate XI.*

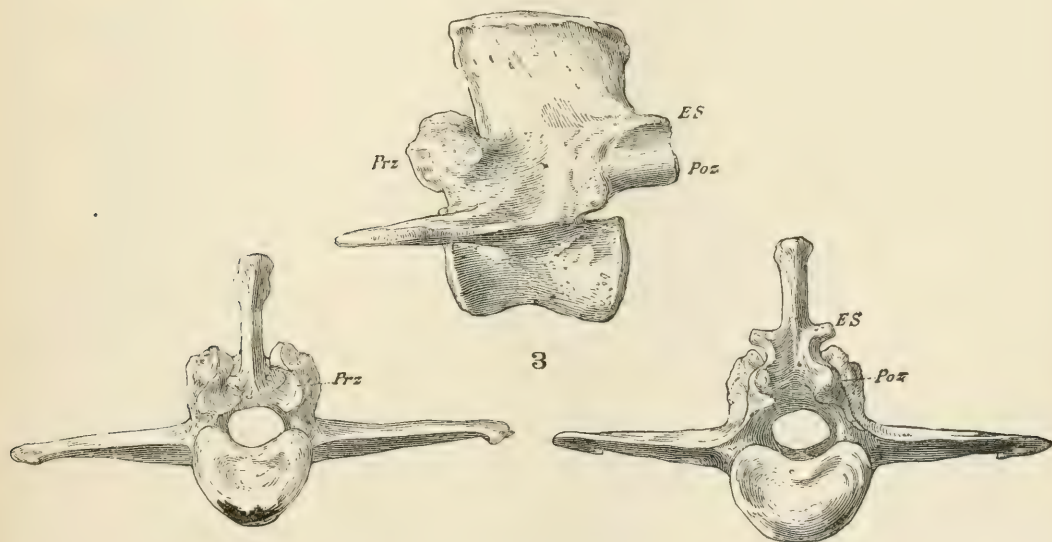
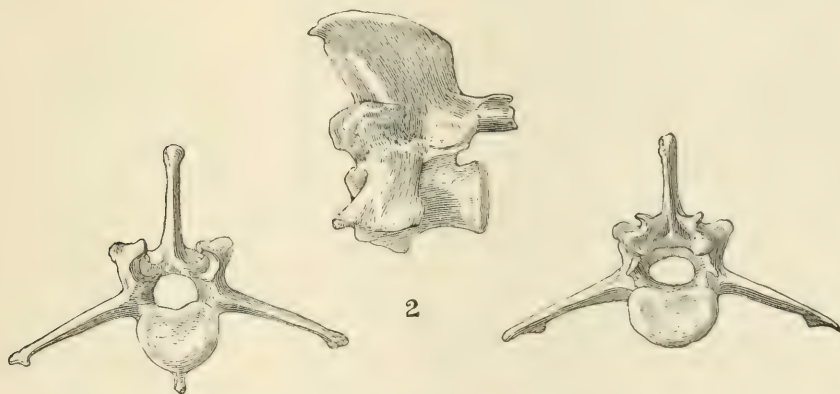
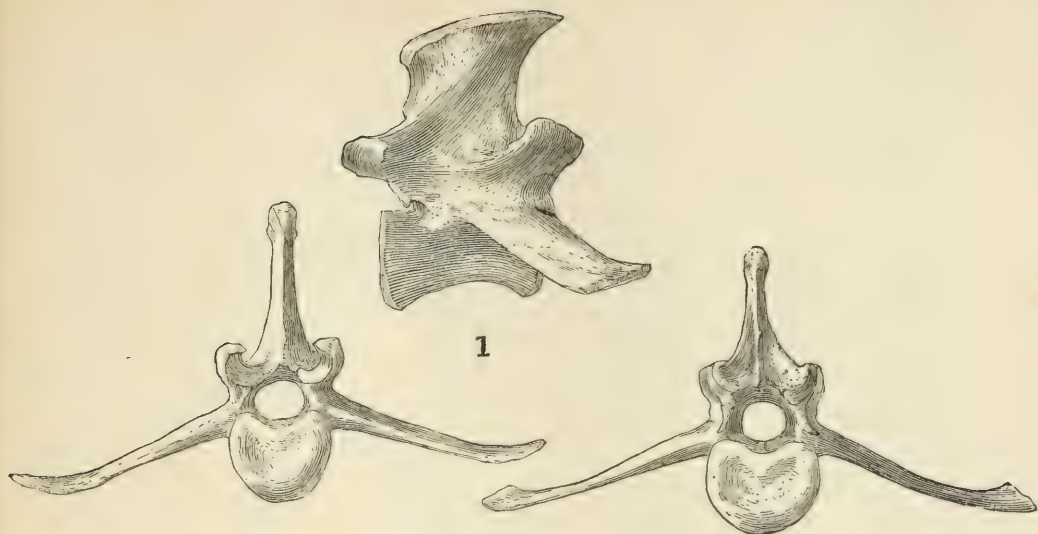
FIG. 1. *Antilocapra americana*.

FIG. 2. *Dicotyles angulatus*.

FIG. 3. *Capra hircus*.

## LETTERING.

*ES*, Episphen; *EA*, epantrum; *Mp*, metapophysis; *Prz*, prezygapophysis; *Poz*, postzygapophysis; *Zgp*, zygapanatrapophysis; *Dp*, diapophysis; *HS*, hyposphen; *Anp*, anapophysis; *h*, humerus; *u*, ulna; *r*, radius.





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## THE EMBRYOLOGY OF *BLATTA GERMANICA* AND *DORYPHORA DECEMLINEATA*.

WILLIAM M. WHEELER.

THE following study of the development of the cockroach and potato-beetle was taken up during the summer of 1887. On the suggestion of Dr. W. Patten, without whose stimulating friendship and assistance the work would not have been undertaken, I began with *Blatta* as a form calculated to help me to a knowledge of the fecundative changes in the Hexapod egg. Dr. Patten kindly placed at my disposal the results of his own work on *Blatta*, in the form of much carefully prepared material and some figures, which I have incorporated in Plate III. (Figs. 43, 45 to 47, 52).

Later I concentrated my attention on *Doryphora*, which I found to be a much more profitable object of study than *Blatta*, especially as far as the more advanced stages were concerned. Thus it happens that my remarks on oögenesis and fecundation are more complete in *Blatta*, while my account of the germ-layers and subsequent stages is carried into greater detail in *Doryphora*.

I have seen fit to treat of both insects as nearly as possible under single headings, instead of describing them independently in two chapters, because they differ strikingly in all the details of development, while their main ontogenetic features are as strikingly similar. By running both descriptions as nearly as possible in parallel lines, the contrasting details are made more salient, while the general remarks may be taken up at intervals and not reserved *en masse* till the end of the paper.

### PREPARATION.

There are three common species of *Blattidæ* in Southeastern Wisconsin: *Periplaneta orientalis* (Linn.), *Platamodes unicolor* (Scud.), and *Blatta germanica* (Linn.). The first and the last occur, as is well known, about houses; the second is abundant under the bark of decaying logs and stumps in open woods.

*Periplaneta orientalis* oviposits from April to August; *Blatta germanica*, at all times during the year. The oöthecæ of *Platamodes* may be collected in great numbers where the insects abound. After many futile attempts to open the oöthecæ of *Periplaneta* and *Platamodes* without injuring the ova, I limited my study to *Blatta*, the egg-capsules of which may be easily opened by the method given below. By careful treatment of the thick-walled capsules of *Periplaneta* and *Platamodes* with a sufficiently strong solution of sodium hypochlorite, it may be found possible to isolate the ova in an uninjured condition.

Specimens of *Blatta germanica* can be obtained at all times of the year from places which they haunt, and with very little attention will live long in confinement. The male is long and narrow, tapering anteriorly and posteriorly; the female is much broader and flatter and uses her wings much less than the male.

Males seem to endure the unfavorable condition of captivity much better than females. When it is desired to time the eggs, the capsule cannot be detached from the female without damage till it has been rotated, and during winter must be kept under a bell jar with plenty of moist blotting-paper to prevent the embryos shrivelling from the dryness of the air.

The ovarian ova in all stages up to maturity were dissected out in normal salt solution and hardened for fifteen minutes in Perenyi's fluid. They were then transferred to 70 per cent alcohol, which was changed several times at intervals of an hour, and were finally preserved in alcohol of the same strength. When stained with borax carmine and sectioned, the yolk retained none of the red stain, while the chromatin of the nucleus shone out as a glistening deep red spot. Perenyi's fluid rendered the chorion of the mature ovarian egg pervious to borax carmine.

Hardening in a saturated aqueous solution of corrosive sublimate gave good results with young ovarian eggs.

Oviposited eggs were killed by placing the capsules in water slowly heated to 80°-90° C. The two lips of the crista of the capsule were then separated by the aid of fine forceps, and pieces of the walls torn away, till the eggs could be easily pushed out of the compartments formed by their choria.

The ova thus isolated were either transferred directly through 35 per cent (10 min.) to 70 per cent alcohol, or they were left for 15 minutes in Kleinenberg's picrosulphuric acid, and after re-

peated washing in 70 per cent alcohol, preserved in alcohol of the same strength. Both methods gave equally good results.

Though I have succeeded in dissolving the chitin of the oötheca with sodium hypochlorite, the method of tearing off the walls after heating to 80° C. gave such satisfactory results that I adhered to it throughout my work.

I have found Grenacher's borax carmine in every way the most expedient and reliable staining fluid. Eggs and embryos up to the time when the cuticle develops were stained before imbedding in paraffine; the sections of other embryos were stained on the slide after attaching them with Mayer's albumen fixative.

The clusters of bright yellow eggs of the potato-beetle (*Doryphora decemlineata*, Say) may be found on the under surfaces of the leaves of the potato-plant during the whole summer, as the insect is polygoneutic.

The beetles, frequently found copulating, may readily be kept in confinement, and will deposit their eggs in the typical flat clusters on the walls of any box or vessel in which they are kept. As I commenced collecting material late in the season, I did not keep the insects in confinement till they oviposited, but collected the eggs from the plant. It was found convenient to cut out the piece of the leaf to which the egg-cluster was attached and to keep it by itself during the process of preparation, as all the eggs of a cluster are in almost exactly the same stage of development.

Beautiful results in preparation were obtained by heating the eggs to 80° C. for 10 minutes in Kleinenberg's picrosulphuric acid (with 3 volumes of water) and preserving in 70 per cent alcohol.

By this process the envelopes, which in the fresh egg adhere closely to the yolk, dilate and stand off from the surface of the egg, and except in the very youngest stages can be rapidly and easily removed with the dissecting needles.

A great number of eggs, heated to 65° C. only, or hardened in cold Perenyi's fluid, corrosive sublimate or simple alcohol, proved to be useless, as the envelopes adhered firmly to the surface of the yolk.

The hot picrosulphuric acid fixes the cells of the embryo in a most satisfactory manner; enough details of the karyokinetic



figures being preserved to enable one to recognize dividing nuclei at a glance. All the eggs were imbedded after treating with clove oil, in paraffine melting at about 55° C. The somewhat gummy yolk cut without any tendency to crumble, and perfect series of sections were obtained without the slightest difficulty.

Staining on the slide with borax carmine gave beautiful results in all stages, but was resorted to only in young eggs, the vitelline membranes of which did not stand off from the surface of the yolk, and in advanced embryos which had developed the larval cuticle. To save time, embryos in other stages were stained before imbedding, after removing the egg-envelopes. As much as possible of the borax carmine was extracted with acidulated 35 per cent alcohol.

#### HISTORICAL.

The cockroaches have long been favorite objects of morphological study. Easily obtained at all seasons of the year, of convenient size for dissection, and being but slightly modified descendants of the oldest insects of geological time, they combine qualifications which make them especially interesting and valuable to the morphologist. Thus we find that no less than twenty investigators have sought material for anatomical and embryological study in the common species of *Blattidæ*. I will mention only those who have treated of the oögenesis and ontogeny of *Blatta* and *Periplaneta*.

Rathke (42) was the first to publish an account of the development of *Blatta germanica*. Brandt (6) made a study of the ovarioles of *Periplaneta*. Huxley's (22) account of the general anatomy of the same insect contains some valuable remarks on the ovaries. Kadyi (23) has given us a condensed account of the oviposition and micropyles of *Periplaneta orientalis*. Patten (38) in 1884 published a preliminary note on the development of *Blatta*. He observed that the first and second maxillæ are at first triramous, and made some remarks on the heart and on the peculiar organs developed from the appendages of the first abdominal somite. Stuhlmann (45) treated of the degeneration of the germinal vesicle in *Periplaneta*. During the same year (1886) also appeared Miall and Denny's work (32) on the anatomy of *Periplaneta*, containing Nusbaum's brief embryological

description of *Blatta*, carelessly written and with figures often grossly inaccurate.

Blochmann's important paper (5), announcing the discovery of polar globules in *Blatta germanica* and two other insects, appeared in 1887. The description of the eggs of *Blatta* is succinct and perfectly accurate.

Of late, Cholodkowsky (10) has published a preliminary paper on the formation of the entoderm in *Blatta*.

*Doryphora decemlineata* has not been investigated heretofore from an ontogenetic standpoint. It is surprising that so common an insect, and one whose eggs present such advantages for embryological study, should have been overlooked. The favored Coleopteron of embryologists has always been *Hydrophilus*, and it is certain that the water-beetles (*Hydrophilidæ* and *Dytiscidæ*) are much less modified forms than the leaf-beetles (*Chrysomelidæ*), to which *Doryphora* belongs.

Nevertheless the development of several Chrysomelids has been studied more or less incompletely.

Packard (35) made a brief study of *Gastrophysa cæruleipennis*, and Melnikow and Kowalevsky (26) studied *Donacia*.

More exhaustive was the attention bestowed on *Lina* by Graber (15), who published his account in the second volume of his text-book on insects (1877). As would be expected from their close systematic affinities, *Doryphora* and *Lina* differ but slightly in their development.

#### OVARIES AND OVIPOSITION.

##### *Blatta*.

The ovaries of *Blatta* are flattened, broadly spindle-shaped masses slung in trabecular connective tissue, continuous with the peritoneum. Each ovary consists of from 14 to 26 ovarioles, or egg-tubes opening into the oviduct. The latter extends backwards towards the median longitudinal axis of the body, and after joining the oviduct from the opposite ovary opens into the broad and short vagina. Besides the tubular colleterial glands the vagina carries on its dorsal face near the proximal ends of the oviduct a thick-walled sac, the spermatheca.

The ovariole has the structure typical in insects. The follicles in all stages of formation are inclosed by the membrana

propria in the form of a tube tapering to capillary caliber at its upper extremity, which is attached to the pericardium. The lumen of the capillary portion is filled with protoplasm in which numerous small nuclei are imbedded. This portion of the ovariole constitutes the germarium. The small nuclei differentiate at the lower end of the germarium, on the one hand into ova, which fill the widening lumen of the tube; and on the other, into flattened epithelial cells, which line the inner surface of the tube, and form the follicles inclosing the ova. There are about ten distinct ova in an ovariole, the lowest being the largest, and the most apical the smallest and most indistinct, those intermediate regularly diminishing in size towards the apex. In *Periplaneta* there are about three times as many ova in an ovariole; but there are only eight ovarioles in an ovary. The lower ova in both species are oval, and are surrounded on all sides by the epithelium, which has grown in between the separate eggs to complete the follicles.

The follicular epithelium (Fig. 5) is composed of large, flat, polygonal cells, with lenticular nuclei which present an intricately coiled chromatin filament and a nucleolus of unusual structure. The latter consists of an irregular mass, not stainable in carmine or methylgreen, and is regarded as plastin by Carnoy (9), who describes and figures very similar nucleoli in the egg-follicles of *Grylotalpa*. The mass of plastin incloses a smaller mass of chromatin, or at least of a substance which does not differ in its reactions from the chromatin of the coiled filament in the same nuclei. In eggs taken from the ovaries just before maturity, when the epithelium is still firmly attached to the underlying chorion, almost all of the nuclei will be found rapidly dividing. Pieces of the epithelium from eggs of different ages were examined in normal salt solution, in methylgreen acetate held for a moment in the fumes of osmic acid, in Rabl's chromformic acid, in Zaccharias' acetic osmic acid; but no traces of an achromatic spindle, or of a regular arrangement of the nuclear filament, so characteristic of karyokinesis could be observed. I therefore conclude that we have here a case of akinesis or direct division. This conclusion is further strengthened by the observation that the nucleolus divides first (Fig. 5 c), and the nuclear wall is constricted during division, an occurrence exceedingly rare in kinetic nuclei, where the nuclear wall

disappears in all but a few of the recorded cases both in plants and animals. Moreover, the two daughter nuclei are frequently very unequal in size.

The chorion (Fig. 1) is a thin, chitinous membrane smoothly covering the surface of the egg. In surface view it appears to be finely granular, the finest granules being arranged in large, more or less regularly hexagonal areas, which are bounded by narrow, dark spaces containing somewhat larger though less dense granules. Each of the hexagonal areas is secreted by one of the polygonal epithelial cells described above. It is only in cross-section that the true structure of the chorion becomes apparent. According to Blochmann (5), — and my observations coincide with his, — the chorion consists of two chitinous laminæ kept in close apposition by means of numerous minute trabeculæ, or pillars. It is the ends of these pillars seen in surface view that look like granules. In the spaces between the hexagonal areas, the trabeculæ are more scattered and individually thicker than those of the hexagons. Hence these lines on the chorion seem covered with larger and more scattered granules. When pieces of the dry chorion are immersed in glycerine and immediately examined under the microscope, the thick liquid may be seen entering the spaces between the hexagonal areas, passing along them in obedience to the laws of capillarity, and then slowly creeping from them on both sides into the adjacent hexagonal areas between their denser trabeculæ. I have also observed that the structure of the chorion of the ripe egg is most distinct in cross-section at the pole directed towards the germarium. Here the two laminæ seen at *oo* in Fig. 4 separate somewhat, and the connecting trabeculæ become longer and more distinct.

I have not been able to trace the formation of the micropyles in *Blatta germanica*. Their structure is easily demonstrated. They are scattered over a quadrant of the upper hemisphere where the beautiful hexagonal pattern of the chorion gives away to an even trabeculation (Fig. 2). The micropyles are wide-mouthed, very oblique, funnel-shaped canals perforating the chorion (Fig. 2 *a*, *b*). The apertures of the funnels appear under a low power as clear, oval spots, the long axes of which are parallel to the long axis of the egg. These perforations are scattered over the micropylar area, sometimes in clus-



ters, sometimes singly. With a higher power the tube of each funnel is clearly visible as a thin canal which dilates rapidly into the large oval aperture on the outer face of the chorion. The narrow tube is sometimes fully as long as the large orifice. The micropylar perforations are all directed from the germarium to the vaginal pole of the egg. Hence a line, the hypothetical path of the spermatozoön, drawn through one of these oblique micropyles, and continued into the egg, would strike the equatorial plane. The female pronucleus, as we shall see further on, moves in this plane.

The micropyles of *Periplaneta*, first described by Kadyi (23), do not differ essentially from those of *Blatta*. In *Periplaneta* the hexagonal pattern is continuous over the micropylar area. The large micropyles, which are more yellowish than the surrounding chorion, are thick walled and not regularly oval, as in *Blatta*, but oblong or subpentagonal. The tube is shorter and terminates on an hexagonal area. Sometimes the micropyles are very close together and seem to overlap.

I have repeatedly sought in vain for a vitelline membrane in the eggs of *Blatta*. Blochmann (5) had no better success. It may exist, but it must be exceedingly thin and inseparably glued to the inner lamina of the chorion.

The colleterial glands of *Blatta* are like those which Huxley (22) and Kadyi (23) have described for *Periplaneta*, a number of long, blind tubes opening into the vagina. They furnish the material for the capsule, viz. : chitin and large crystals of calcium oxalate. In *Blatta* these glands are glistening white till the time of oviposition approaches; when they assume a yellow tint, and the octahedral crystals are seen imbedded in a viscid substance which fills their lumina. This viscid substance is soluble in potassium hydrate, and is consequently not chitin. When excreted to form the oötheca, it slowly hardens, deepens in color, and becomes insoluble in potassium hydrate. Light has nothing to do with this change, which is possibly produced by the oxygen in the air. It is the same change which is undergone by the cuticula of the insect itself immediately after ecdysis.

I have made a few observations on the oviposition of *Blatta germanica*, similar to those published by Kadyi (23) on *Periplaneta orientalis*.

When about to form the capsule, the female *Blatta* closes the genital armature, and the two folds of the white membrane which lines the oöthecal cavity close vertically in the middle line. Then some of the contents of the colleterial glands are poured into the chamber and bathe the inner surface of the posterior wall. The first egg glides down the vagina from the left ovary, describes an arc, still keeping its germarium pole uppermost, after having pressed the micropylar area against the mouth of the spermatheca, passes to the right side of the back of the chamber, and is placed perpendicularly two-thirds to the right of the longitudinal axis of the insect's body. The next egg comes from the right ovary, describes an arc to the opposite side of the body, decussating with the path of the first egg, and is placed completely on the left side of the median line. The third egg comes from the left ovary, and is made to lie completely on the right side of the median line: and so the process continues; the ovaries discharging the eggs alternately, and each egg describing an arc to the opposite side of the capsule. In females killed during oviposition each oviduct will be found distended with eggs, often two or three end to end, increasing the length and breadth of the lumen to an abnormal degree. Gentle pressure of the female's abdomen between the thumb and finger will sometimes cause the insect to oviposit a few eggs, the paths of which can be seen to decussate.

The oöthecal chamber soon becomes too small to contain all the constantly accumulating eggs, so the anal armature opens and allows the end of the capsule to project. A raised line, the impression of the edges of the white membrane, runs down the end of the capsule. The last egg deposited comes from the right ovary and lies two-thirds on the left and one-third to the right of the median line. Thus the first and last eggs laid lie with their greater bulk on opposite sides of the median vertical plane of the capsule, and serve to commence and close the series and round off both ends of the capsule. Owing to their being crowded up against the walls of the capsule, they acquire quite a different shape from the remaining symmetrically and alternately deposited ova. They develop normally, however, the embryo appearing on the inner obtuse edge. As soon as the last egg is laid, a further discharge from the colleterial glands spreads over the vaginal or anterior wall of the cavity,

and becomes evenly continuous with the secretion which has before been spread over the back and the sides of the capsule by the white membrane. When the anterior end of the capsule is examined, the escutcheon-shaped vaginal opening is found to have left its impression even to the delicate wrinkles into which the surrounding cuticula was thrown by the closing of the orifice. This end of the capsule is white, gradually shading into the brown of the opposite end.

The crista, a cord-like ridge running the full length of the dorsal surface of the capsule, is a thick-walled tube, either half of which is formed by the edge of the side walls of the capsule split into two laminæ (Fig. 3  $o^1, o^2$ ). The rhythmical clasping of the three pairs of palpi, which guard the vaginal opening, is registered in an exquisite pattern on the inner face of either half of the crista.

The canal is filled with a vacuolated substance (Fig. 3 *cp*) which at first sight resembles the yolk of the egg, but when examined more closely is seen to have quite a different structure and origin. In the egg ready to leave its follicle the epithelium is much thickened at the germarium pole into a biconvex-lens-shaped cap (Fig. 4), the cells of which are not flat like those on the other portions of the egg, but long, columnar, and more or less curved. The two laminæ of the chorion spread apart beneath this cap and dilate into a pear-shaped sac divided up into numerous polygonal chambers by delicate chitinous partitions (Fig. 4 *b*). While the egg is leaving the follicle, the epithelium at the lower pole is loosened from the chorion, and the egg protrudes into the oviduct. As it advances, the epithelium is rolled back and doubled up in folds till it is freed from the chorion as far as the cap. Then it breaks, letting the egg pass into the oviduct with the thick cap of cells firmly attached. The egg is placed in the capsule, and the cap comes to lie in the crista, filling its lumen. The large nuclei degenerate, and soon entirely disappear, the protoplasm becomes dry and vacuolated, and finally transformed into the yolk-like mass described above. This substance probably serves as a cement to keep the lips of the crista in contact till separated by the emerging larvæ. Thus a small portion of the follicular epithelium, that portion which corresponds to the nourishing cells in other insect ovaries, is deposited with the egg. To my knowledge

this has not been observed in any other arthropod eggs heretofore described, excepting *Musca* (Bruce, 7). The pear-shaped dilatation of the chorion is directly over the head of the future embryo and hatching insect, and is possibly more easily ruptured or dissolved than the surrounding chorion.

Of 40 capsules examined for the purpose of noting which ovary sent out the first and which the last egg, 32 commenced with the right egg (from the left ovary) and closed with the left egg (from the right ovary), six capsules commenced and closed with the right, and one commenced and closed with the left egg. Evidently the 32 were normal; in the insects which deposited the six, one of the ovarioles was probably either atrophied or wanting, though the perfectly alternate arrangement of the eggs in the capsule was in nowise interrupted on this account. The two remaining egg-capsules were small and abnormal.

The number of eggs in a capsule, far from being constant in *Periplaneta orientalis*, is even more fluctuating in *Blatta germanica*. In 34 capsules counted the average number was about 40, the least number 28, and the greatest 58. The number varies in different localities and is doubtless dependent on the food of the female insect. In several capsules obtained where amylaceous food was abundant the average was much higher than in a much greater number of capsules obtained from a place where fatty food was the only diet.

The above description of the oviposition of *Blatta germanica* probably applies to most species of the *Blattidae*. But this species differs from *Periplaneta* and probably many other forms, in rotating the capsule, a process now to be described. As soon as the last egg has passed the vagina and been placed in the capsule, the latter begins to rotate on its longitudinal axis, till the crista has described one-fourth of a cylinder to the right. The capsule is now in a horizontal position having its greater transverse diameter parallel with the corresponding transverse diameter of the insect's body. The abdomen contracts during oviposition, and its end comes to lie anterior to the tips of the wings, so that the broad ends of the latter hide and protect the protruding end of the capsule. The rotation requires about a day. In one case a female kept the capsule in a vertical position for two weeks, apparently from some inability to revolve it. In



all other cases the capsule was regularly turned to the right, never to the left.

The female *Periplaneta orientalis* drops the capsule soon after its completion, with predilection in some food supply, such as flour or meal. *Blatta germanica* carries it for about a month, then drops it shortly before the hatching of the larvæ. Some writers claim that the parent assists the young in escaping from the capsule, but I have proved by many experiments that the expanding and struggling of the young insects are amply sufficient to separate the feebly united lips of the crista. Such an instinct in the female would be of use only if the lips of the capsule could not be opened by the young. Taschenberg (46) claims that the female regularly lays only one capsule and dies soon after its deposition. My observations on fifty females, whose wings were clipped as soon as they had formed their first capsule, have convinced me that they certainly lay two perfect capsules as a rule, and possibly more, in the course of the year.

As will be seen from the preceding account, it is a very easy matter to orient the eggs of the capsule, to tell just what position any oöthecal egg held in the ovary, or just what position any egg in the ovary will hold in the capsule. The germarium pole of the ovarian egg lies just beneath the crista after oviposition. The concave side of the curved sausage-shaped ovarian egg is turned to the wall of the capsule, and its convex face, on which the embryo will appear with its head towards the crista, is turned to the interior of the capsule and faces the corresponding surface of the opposite egg. The micropyles which pointed away from the germarium are on the convex face of the ovarian, and on the inner face of the oöthecal egg, and point downwards away from the crista.

#### THE DEVELOPMENT OF THE EGG TO THE FORMATION OF THE BLASTODERM.

##### *Blatta.*

The oöthecal egg of *Blatta*, like the ovarian egg, is glistening white. The latter has been described as sausage-shaped, but the pressure exerted by the eggs on one another in the capsule alters their original form very considerably. They assume the

shape of half an elliptical disc, the short axis of which is to the long axis as 2 is to 3, with a thickness one-sixth of the short axis (Figs. 36 and 37). The egg is about 3 mm. long, 1 mm. broad and  $\frac{1}{3}$  mm. thick. Its volume is therefore almost a cubic millimeter. The cephalic end (Fig. 36 *c*), recognized by its evenly rounded contour, is immediately beneath the crista of the capsule. The opposite or caudal end (Fig. 36 *s*) is distinguished by a slight sinus. The ventral face is traversed by a keel which runs from the cephalic to the caudal extremity and is most pronounced a short distance below the middle of the egg. The dorsal surface is flat and evenly curved anteroposteriorly. Cross-sections of the ovum are consequently pentagonal (Fig. 40). Thus the eggs can be easily oriented, and they have a great advantage over spherical or even oval ones, in that all the earliest developmental changes can be traced directly to their relationship with the parts of the future embryo. This is of the highest importance in the early stages.

It will have been observed that a complete reflexion of the egg takes place during oviposition as the concave face of the curved ovarian egg becomes the convex back of the oöthecal egg, and the convex micropylar face of the former becomes the straight, carinated, ventral face of the latter.

*Yolk.* — I have not been able to observe a passage of follicular epithelial cells into the egg to form yolk by their disintegration, as has been described by Will (51) in *Nepa* and *Notonecta*, and by Ayers (1) in *Æcanthus*. There is only one layer of cells in the follicular epithelium of *Blatta*, and as this persists till after the chorion is completed, no migration of nuclei into the yolk, or even disintegration of nuclei at the surface of the egg, is observable. All of the yolk in *Blatta* (excepting those portions derived from the germinal vesicle?) is secreted by the protoplasm of the epithelial cells, not as yolk, but as substances which are taken up by the growing ovule, and again secreted in the form of the bodies to be described presently. During this process of yolk-secretion, the epithelial cells remain intact, their slow disintegration not taking place till after oviposition, when their compacted and yellowish remains have assumed the appearance so suggestive of the *corpora lutea* of the Mammalia.

The yolk of the eggs of *Blatta* has been studied by Patten

(38) and Blochmann (5). The former has described the physical structure; the latter, the peculiar bilateral distribution of the yolk elements. Though my researches have revealed only a few new facts concerning the yolk, I will give them in their entirety.

In the young ovarian egg, 0.5 mm. long, the nucleus is surrounded by granular protoplasm in which no yolk has developed. In eggs 1 to 2 mm. long the yolk consists of two kinds of bodies: transparent fat globules of various sizes, and a translucent albuminous substance broken up into distinctly outlined masses which are polygonal in form from mutual pressure. Beneath the follicular epithelium is a layer of small albuminous masses enveloping the interior yolk. This is at a time when the large nucleus is disintegrating. By the time the egg has reached its full size, the yolk has assumed the highly differentiated structure best studied in the oöthecal egg.

The yolk of a fresh mature egg crushed between the slide and the cover glass in its own liquids, or in normal salt solution, shows an abundance of different sized highly refractive oil globules, and a greater number of distinctly outlined albumen spheres, which are polygonal in the intact egg where mutual pressure prevents them from taking on the spherical shape which they seem to be continually striving to assume. These albumen spheres are thin-walled sacs full of a thin liquid in which float multitudes of small, irregular granules. Sometimes small oil globules are enclosed. That the contents of these sacs is a thin liquid is proved by the exceedingly active Brownian movement of the irregular granules, a movement which is certainly constant in almost all these vitelline bodies in the living egg. But these bodies are far from being alike in structure. In some few the granules are very minute, closely packed, and exhibit no Brownian movement; in others the granules are large and distinctly irregular, few in number, and possessed of a tendency to unite in flakes which hang suspended in the thin liquid filling the sacs. In the great majority of these bodies, however, the mean between these two extremes in structure is maintained. It is probable that the granular forms arise from the dense homogeneous bodies by chemical decomposition. This decomposition, which is accomplished, as I said above, in the ripe ovarian egg, takes place in different parts of the egg in different degrees,

thus bringing about the peculiar bilateral structure first noticed by Patten and subsequently described by Blochmann. In hardened eggs the granules have the appearance of nets with larger or smaller meshes (Figs. 23, 24, etc.). This structure is best seen in cross-sections of eggs hardened in alcohol or picrosulphuric acid.

For the distribution of the above-described yolk-elements in the egg I cannot do better than quote Blochmann's succinct and accurate account. He says: "Die Hauptmasse des Dotters erscheint auf dem Querschnitt [see my Fig. 40] etwa als gleichschenkeliges Dreieck, das seine unpaare (kurze) Seite nach aussen, seine Spitze der Mitte zukehrt. Diese Dottermasse besteht aus durch gegenseitigen Druck polygonal abgeplatteten Körpern, deren Umrisse besonders an den peripheren Partien deutlich sind, während sie in der Mitte des Eies mehr oder weniger zusammenfliessen. In den peripheren Regionen zeigen diese Körper eine feine Granulirung ihrer Substanz, während sie im Innern des Eies vollständig homogen erscheinen. Sie färben sich bei der gewöhnlichen Behandlung mit Boraxkarmin ziemlich intensiv. Umgeben wird diese Dottermasse von einer Zone [my Figs. 39 and 40] von ebenfalls polygonalen Elementen, die jedoch überall deutlich unter sich und von den Elementen (der Hauptmasse des Dotters) sich abgrenzen. Sie zeigen eine grobnetzige Struktur und färben sich mit Boraxkarmin nur ganz wenig. Diese Zone des Dotters hat ihre grösste Dicke über der Spitze des von dem anderen gebildeten Dreiecks und nimmt nach den Seiten zu ab, um in der Mitte der Rückseite wieder etwas an Mächtigkeit zu gewinnen. Dieser blasse Dotter bildet also einen kontinuierlichen Mantel um den anderen. (Es) finden sich längs der ganzen Eioberfläche zwischen die blassen Dotterkörper eingelagert einzelne stärker färbbare Elemente des Dotters (der Hauptmasse) oder auch kleine Gruppen von solchen. . . . Unregelmässig durch beide Dotterarten finden sich zahlreiche grössere und kleinere Fetttropfen, die an den Präparaten als Hohlräume erscheinen, da das Fett durch die Behandlung mit Chloroform, Terpentinöl, etc. aufgelöst wird" (my Figs. 23, 24, etc.).

The ventral thickening of the "continuous mantel" of granular yolk polyhedra, which surrounds the wedge-shaped central mass



of translucent polyhedra, is a pre-arrangement for the reception of the blastoderm, and more particularly the future embryo. The vital activities, which, in forming the embryo, finally become centred on the ventral face of the egg, find the yolk here already sufficiently decomposed to admit of easy metabolism into protoplasm. Later, in eggs with advanced embryos on their ventral faces, the granular yolk has again become transparent and homogeneous in extensive masses which arise from the confluence of many of the polyhedral bodies. I differ from Blochmann in maintaining that the granular yolk is originally derived from the homogeneous variety. He was led to infer the opposite process from his study of the yolk in ants' eggs.

*Protoplasm.*—In young ovarian eggs, 0.25 to 0.5 mm long, the cytoplasm is finely granular. The deutoplasm begins to accumulate, and by the time the egg has become 1 mm long, the above-described vitelline bodies and oil globules have developed in such numbers as to reduce the protoplasm to an exceedingly delicate net. In the mature egg the *Keimhaut* described for so many insects' eggs is a layer so thin that it is just perceptible on the centre of the dorsal surface and at the cephalic pole (Fig. 4 *pr*). This protoplasmic layer is full of what I shall call Blochmann's corpuscles. They are minute rod-shaped bodies so numerous in the surface protoplasm as to make it appear reticulate. They look like bacillar micro-organisms, stain deeply, and according to Blochmann, who is probably right in thinking that they play an important role in the development of the egg, multiply by transverse division (like Bacteria). Weismann was the first to note these bodies in Diptera in 1863. Blochmann (3, 4) called attention to them in 1884 and 1886, in the eggs of *Camponotus* and *Formica*, and in 1887 in *Blatta*, *Periplaneta*, *Pieris*, *Musca*, and *Vespa*. In the three last genera the bodies are spherical. In several of Stuhlmann's (45) figures, these bodies are prominent. In *Blatta* I have found them wherever the peripheral layer of protoplasm is perceptibly thickened, especially surrounding the polar globules on the middle of the dorsal surface (Figs. 14, 15, and 16), and at the cephalic end of the egg (Fig 4 *pr*). They seem to be made of more rigid material than the protoplasm in which they are embedded, for they protrude as very minute prickles from the surfaces of eggs hardened in Perenyi's fluid. I have not been able to trace out their derivation and ultimate destiny.

As the granular yolk polyhedra of the ventral portion of the egg are much smaller than the homogeneous ones of the interior, there is more protoplasm in the ventral part of the egg. The internal portions crumble very easily in sectioning, and I am hence inclined to think that very little or no protoplasm extends in between these bodies from the periphery. Thus we see that the distribution of the protoplasm, as well as the yolk, is in accordance with the position of the future embryo. Later, when cells appear in the egg, their amœboid cytoplasm consists of evenly granular protoplasm, faintly stainable in borax carmine.

*Karyography of the Egg.*—In studying the changes in the nucleus, it has proved to be impossible to preserve the finest cytological details, since the ovarian eggs of *Blatta*, like the eggs of the Orthoptera in general, are not easily sectioned unless hardened in Perenyi's fluid, as the yolk is exceedingly friable. Perenyi's and Kleinenberg's fluids do not preserve the karyokinetic figures perfectly, but cause the loops of chromatin to fuse in masses. On the other hand, the achromatic spindles are often beautifully distinct. Any discrepancy between Blochmann's figures of the polar globules and mine, is probably to be attributed to a difference in the use of reagents.

In young and transparent ova taken from the middle of the ovariole, the nucleus is seen to have reached the acme of its development in volume. It is a large spherical body, more highly refractive than the surrounding cytoplasm. Its fluid contents, the karyoplasm, is distinctly separable into two substances, a liquid karyochylema and an achromatic (plastin?) reticulum. In the meshes of the latter is suspended a third substance, the deeply stainable chromatin, in one large and several smaller masses, or in several small irregular particles derived from the former by disintegration. The nuclear wall is very distinct. Whether it is a membrane or merely a peripheral inspissation of the karyoplasm is uncertain. When ovarioles are treated with Fol's picrochromic acid or Merkel's chromplatinum solution, the whole nucleus contracts and leaves a meniscoid cavity between itself and the cytoplasm, though it still preserves its distinct and evenly spherical contour.

In all the following stages the egg, having become opaque, must be studied in sections, and the history of the nucleus con-

structed from a series of isolated observations. While the yolk is accumulating, the nucleus becomes amœboid, leaves its position at the centre of the egg, and travels to the surface. The egg is at this time very slightly curved, and the nucleus always passes to the centre of the concave side. This amœboid nucleus is seen in Fig. 6 just after reaching the surface. It is still large, and does not stain more deeply than the surrounding yolk bodies. Its long axis is parallel to the long axis of the egg. The chromatin, in large masses in the younger egg, has been reduced to numerous granules of varying size, still recognizable as chromatin because staining deeply in borax carmine. The pseudopodia are now drawn in, and the nucleus becomes spheroidal. Soon the face in contact with the surface becomes cup-shaped, and round masses of a homogeneous substance indistinguishable from the surrounding yolk bodies fill the cavity (Figs. 7 and 8 *b*). In this stage the nucleus is probably giving off the "maturation spheres" (Reifungsballen), which Stuhlmann saw given off from the nucleus of so many insects' eggs (notably Lepidoptera); Will (51) also describes this process in Hemiptera. In many insects Stuhlmann found that these spheres differed from the surrounding yolk bodies in power of refraction, etc. The concavity (Einbuchtung) of the nucleus in *Blatta* often contains several of these spheres. Figure 8 represents such a nucleus seen from the surface, the plane of section being at right angles to the plane of section in Figs. 6 and 7. Here the concavity is composed of separate cavities which have fused. The maturation spheres, after their escape from the nucleus, mingle with the yolk bodies. Above the orifice in Fig. 8, at *pn*, is a small body, denser and more refractive than the surrounding plasma. I think it corresponds to Stuhlmann's paranucleolus. In its centre is a deep red body, probably a granule of chromatin. In Fig. 9 is seen a nucleus containing two paranucleoli, *pn*, destitute of the central granule. I cannot say what becomes of these bodies. They do not appear in all nuclei (*confer* Fig. 7), and are probably evanescent structures formed and again disintegrated during the mysterious process of nuclear degeneration. In Fig. 9 granules of chromatin, most numerous near the point *n*, are scattered through the karyoplasm. The disintegration of the nucleus by giving off the maturation spheres progresses till, when the egg is about 2 mm. long, it is

reduced to a small, somewhat crescentic body, which, unless its position has been marked, is easily mistaken for a yolk body, as it in no way differs from the surrounding yolk in ability to take up coloring-matters. Hence it happens that many investigators have supposed the insect egg to become enucleate at this time. The resemblance between a yolk polyhedron and the remains of the germinal vesicle is greatly increased by the granular contents of both. In the germinal vesicle these granules are the comminuted remains of the large masses of chromatin so conspicuous in the young egg; in the yolk bodies they are albuminous substances destined, like the other yolk materials, to become food for the protoplasm. At the very spot where the nucleus degenerated, viz. at the middle of the concave side of the egg, there appears in eggs almost mature (2.5–2.8 mm. long), a cluster of numerous chromatin granules, which I believe to be the same as those in the germinal vesicle, grown more conspicuous by aggregation. Stuhlmann has figured several bodies like my Fig. 10, representing this aggregation which has progressed considerably in the centre. These chromatin granules are probably uniting to form filaments preparatory to karyokinesis. The aggregation takes place in such a way that in eggs treated with Perenyi's fluid a narrowly oblong mass of chromatin is formed, an appearance undoubtedly due to the fusion of the separate filamentous loops. The oblong mass is represented in Fig. 11. When the outlying granules have been added to it, and the achromatic fibrillæ have made their appearance, the first polar spindle in the metakinetic stage is completed (Fig. 12). The axis of the spindle is directed at right angles to the surface of the egg, which is now mature though still enveloped in the follicular epithelium. In Fig. 13 the equatorial plate has divided transversely, whether by longitudinal fissure of the individual loops or not, I am unable to say, and the two masses of chromatin are on their way to the poles of the spindle. Arrived at the poles the masses become spherical, and the achromatic spindle fades away, while the outer sphere of chromatin surrounded by a mass of protoplasm full of Blochmann's corpuscles is almost constricted off from the egg to form the first polar globule. While this is taking place the egg is being freed from all its epithelium, except the cap at the cephalic pole, impregnated and placed in the capsule. The daughter nucleus of the



first polar spindle remaining within the egg now forms another spindle directed like the first. This is seen in Fig. 14. The blade of the microtome has somewhat raised the loosely attached first polar globule, the protoplasm of which is seen to contain many of Blochmann's corpuscles. The karyokinesis of the second spindle progresses in the same manner as the first and the second polar globule is given off, also surrounded by bacillar protoplasm. The portion of the nucleus which becomes the female pronucleus, is not seen in Fig. 15, where only the two polar globules are represented, as it appears in the next section. Figure 16 is from a surface view of the polar globules. By comparison with Fig. 14 *p<sub>gl</sub> 1* it will be seen that they are lenticular. Here the female pronucleus appears as a more indistinct body (because out of focus) lying between the polar globules. The polar globules which I have been able to find in many eggs taken from the capsules while they were still vertical in the genital armature (about 6 to 12 hours after the beginning of oviposition) lie in the middle of the convex dorsal wall of the oöthecal egg. They do not divide subsequently to form what Weismann (48) calls secondary polar globules, but soon disintegrate. In eggs about one day old their remains may be found as an amorphous granular mass, lying just beneath the chorion and entirely separated from the egg.

The female pronucleus increases considerably in size before leaving the surface of the egg (Fig. 17 ♀ *pn*). This increase is gradual but constant as it makes its way through the dense yolk of the interior of the egg to the apex of the isosceles triangle of homogeneous yolk abutting on the back part of the granular ventral yolk. It is on this journey that the female pronucleus meets the male pronucleus formed from a spermatozoon which has entered the egg by one of the funnel-shaped micropyles on the upper ventral face.

Though I have succeeded in throwing a little more light on the copulation of the pronuclei than Blochmann, I cannot regard my observations as completely satisfactory. The process must be studied in Arthropod eggs with more evenly compact yolk than the eggs of Orthoptera, the numerous cracks and fissures in which render the observation of delicate internal processes exceedingly difficult if not impossible. Moreover, the copulation of the pronuclei in *Blatta* is hurried through very rapidly.

In more than a hundred eggs which I sectioned from capsules 6 to 24 hours old I found the greater number in the polar globule stage and all the remainder, with two exceptions, in the stages just before, during and after the division of the cleavage nucleus. In the two exceptions which I describe and figure I found what I take to be the pronuclei. The arrows in the figures point in the direction of the long axis of the egg, only the circumnuclear portions of which are represented.

In Fig. 19 the female pronucleus is about one-third the distance from the cephalic end instead of being in the middle of the egg where the polar globules are formed. It is no further from the dorsal surface than the female pronucleus in Fig. 17, but is much larger. Hence I believe it has travelled up along the dorsal surface to meet the male pronucleus (Fig. 19 ♂ *pn*), which has advanced through almost the whole dorsoventral diameter of the egg. The female pronucleus exhibits the usual coiled chromatin filament. The male pronucleus is granular, of somewhat irregular outline, and surrounded by vacuolated protoplasm. It is rather deeply stainable in borax carmine. In this Fig. 19 the pronuclei are of very different size, and notwithstanding the male pronucleus has passed through three-fourths of the dorsoventral diameter, a distance of  $\frac{3}{4}$  mm., it has not increased much in volume when compared with the mass of the long though attenuated head of the spermatozoon from which it originated. No astral radiation could be seen surrounding these pronuclei. In Fig. 20 we have what I take to be the two pronuclei conjugating. The smaller presumably male portion of the compound or cleavage nucleus is larger than the male pronucleus in Fig. 19. The place of union is about the middle of the homogeneous yolk, *i.e.* about one-third of the dorsoventral diameter from the back of the egg. The nuclei of Fig. 19 would probably have fused at a point near the dorsal surface one-third the distance from the cephalic to the caudal pole, but the paths of these two nuclei were undoubtedly aberrant. My observations on single female pronuclei and cleavage nuclei found at various points along the median dorsoventral diameter lead me to conclude that the middle of the homogeneous yolk is the normal point of conjugation. I have represented (Fig. 18) another female pronucleus from near the point of fusion because its structure is different from that of the other female pronuclei

figured. Its chromatin is limited to a few filaments; whereas in Fig. 19 ♀ *pn* we have a long and intricately wound coil.

The cleavage nucleus continues the course begun by the female pronucleus. Figure 21 represents it when it has reached the middle of the dorsoventral axis. The cytoplasm surrounding this nucleus, which is drawn from an egg hardened in picrosulphuric acid, shows an astral radiation. The cytoplasm passes by insensible degrees into the surrounding homogeneous yolk substance. It is as if the female pronucleus when it left the polar globules took a little mass of the protoplasm abundant at that part of the egg's surface and travelled with it, making it convert the yolk into protoplasm during the journey.

As soon as the cleavage nucleus reaches the front edge of the mass of homogeneous yolk, or has advanced a very short distance further into the granular yolk, it stops and begins to increase in size till it becomes a clear vesicle (Fig. 22) in which the chromatin, broken into irregular fragments, lies scattered through the finely granular contents. The nuclear wall grows fainter and disappears. The large spindle now appears, and the typical process of karyokinesis is carried on (Fig. 23). The polar axis of the spindle was in all but one of the many cases in which I observed the division, parallel to the long axis of the egg. In the exceptional case (possibly an abnormal egg) it was parallel to the dorsoventral diameter. Even before the division of the nucleus commences, the polar axis of the future spindle is foreshadowed, as it were, in the shape of the granular (amœboid) cytoplasm, which, as may be seen in Fig. 23 *cp*, is elongated in a direction parallel to the cephalocaudal axis of the egg. The karyokinetic process employed in this and the subsequent divisions is typical. Soon after the nuclear wall again makes it appearance the two nuclei with the cytoplasm which surrounds them separate about one-fifth the longitudinal diameter of the egg, and then prepare for the next division. The polar axes of the two daughter spindles now formed are very nearly at right angles to the polar axis of the mother nucleus.

In all the first divisions the perfect isochronism of the different stages in the different nuclei is striking. Fig. 24 represents two spindles from an egg containing four nuclei in exactly the same (metakinetic) stage. In this figure, taken from a longitudinal section, one of the spindles (*c*) has its axis at right angles

to the longitudinal and also to the dorsoventral axis of the egg. The loops forming the equatorial plate are readily seen and counted. Ten in number, each probably attached to an achromatic fibril, they are arranged in such a manner that seven form a circle inclosing the remaining three.

The divisions of these four products of the cleavage nucleus continue till about 60 to 80 cells have been formed, scattered irregularly through the granular ventral yolk. The axes of the spindles are inclined in various directions, and nothing indicates an early differentiation into cells destined on the one hand to remain in the yolk, and on the other to form the blastoderm.

The numerous amœboid cells next migrate to the surface of the egg. In Fig. 25, representing the ventral third of a median cross-section, two of these cells have just reached the surface, while one is still on its way. On reaching the surface the cells first become somewhat conical, and then gradually flatten out. The tension of the cytoplasm is so great that the inclosed nucleus is forced to become lenticular (Fig. 26 *a*). The cells which have reached the surface, and are much scattered over the roof-shaped ventral face and the adjacent portions of the lateral faces, commence dividing tangentially, not by karyokinesis, as heretofore, but by akinesis. Figure 36 represents the lateral surface view, and Fig. 26 part of a transverse section of an egg in this stage. The division of the nuclei which have reached the surface is very rapid, and compact colonies of cells of different sizes and in different stages of the unequally constricting process characteristic of akinesis may be seen embedded in amœboid masses of protoplasm. I have given such a syncytium (enlarged from Fig. 36) in Fig. 34, and two of the dividing nuclei from other parts of the same egg in Fig. 35 *b, c*. The method of division is exactly like what was described above for the cells of the follicular epithelium (Fig. 5), omitting the peculiar nucleoli which I have not been able to detect in these nuclei. My observations tend to show that all the future divisions in the formation of the blastoderm and those subsequently undergone by the serosa are akinetic, the densely coiled chromatin filament remaining inert, and the division taking place by a constriction which often produces two daughter nuclei of very unequal size. I emphasize the fact that these forms of division could not have



been produced by reagents, as these eggs were hardened in picrosulphuric acid or simple alcohol, which in younger and older eggs preserve the karyokinetic figures of the cleavage nucleus and its immediate descendants with great clearness.

The nuclei of the small syncytia spread apart evenly over the surface of the egg, which now presents the appearance of Fig. 37. The pseudopodia of the amœboid cytoplasmic masses run together to form a net. The egg is now in the blastema stage of Patten (38). The cells at the surface are being continually reinforced by cells migrating from the yolk. Ever since the first division of the cleavage nucleus the nuclei have undergone a gradual and steady diminution in size, and this progresses till the formation of the blastoderm which takes place by the division of the blastema cells. In this stage the yolk is covered with a layer of protoplasm, imperfectly divided into small cells, each containing a lenticular nucleus, which in turn contains two very deeply stainable nucleoli (Fig. 33). Fig. 27 is a transverse section through the front of an egg in the blastoderm stage. All the protoplasm at the surface of the egg is carried there by the migrating cells or formed from the surface yolk through their influence, as the *Keimhaut*, so highly developed in *Doryphora*, as will be seen further on, is undeveloped on the ventral, lateral, and all but a very small portion of the dorsal surface of the egg of *Blatta germanica*.

*All the nuclei, formerly in the yolk, probably rise to the surface to form the blastema and reinforce it in its formation of the blastoderm.* Before the blastoderm is completed, cells separate from it and pass inwards to form the yolk cells, or vitellophags. The following are my reasons for believing that all the products of the cleavage nucleus go to the surface. The cleavage nucleus cells have large pale nuclei and distinctly amœbiform cytoplasm, like those in the yolk of Figs. 25 and 26. Subsequently none of these nuclei are to be found in the yolk, but in their stead occur at greater or lesser distances from the ventral and lateral faces small deeply stainable nuclei of exactly the same size as the blastoderm nuclei, not surrounded with amœbiform cytoplasm, but apparently melting their way through the yolk, often in the middle of a dense yolk body, and, above all, exhibiting the same intimate structure as the blastoderm nuclei (Fig. 28). When treated with picrosulphuric acid, these centrip-

etal nuclei show the two highly refractive nucleoli of the surface cells; when treated with alcohol only, both the surface and yolk nuclei exhibit the same closely wound, deeply stainable chromatin filament. Such exact similarity in size, shape, and minute structure is very strong evidence in favor of community of origin. Still I have not been able to find an egg without nuclei in the yolk, notwithstanding I sectioned many eggs in the blastoderm stage. I am inclined to think that such a stage may not occur, but that the last of the cleavage nucleus products go to the surface simultaneously with the passage in the opposite direction of the first blastoderm products. Thus the enucleate yolk stage would be slurred over.

The time required for the development so far described is approximately as follows: The first polar spindle is formed in the ovaries; the second polar spindle during oviposition. Both polar globules have been constricted off by about the sixth hour from the commencement of oviposition. By the end of the first day the female pronucleus has fused with the male pronucleus, and the cleavage nucleus thus formed has reached the back of the granular ventral yolk. The products of the cleavage nucleus are formed and reach the surface by the end of the third day. By the end of the fourth day the blastema is completed. During the fifth day the blastema nuclei proliferate and complete the blastoderm by the close of the sixth day. The development is, of course, accelerated by a rise and retarded by a fall in temperature, though not to the extent observed in many other animals.

Before passing over to a description of the early stages of the egg of *Doryphora*, I will recapitulate the movements of the nuclei by means of diagrams of a longitudinal and equatorial cross-section of the egg (Figs. 39 and 40). In these diagrams *a* is the cephalic, *b* the caudal end, *c* the ventral, *d* the dorsal, *o* the lateral surface. The shaded body *p* is the homogeneous yolk, the dotted portions *r* the granular yolk. The germinal vesicle starting from the central point *e* goes to the surface, describing the path represented by the line *ef*. Here it gives off by two successive divisions the two polar globules *f*<sup>1</sup> and *f*<sup>2</sup>, and then as the female pronucleus turns back to go in the opposite direction. The line representing the passage of the germinal vesicle to the surface is really too long,

as this path is travelled over when the egg is much smaller, and the distance from the centre to the periphery much less than in the mature egg. The nucleus of the spermatozoon entering the egg at some point on the ventral surface between *s* and *c*, probably at or near *h*, advances through the egg as the male pronucleus *i* and fuses with the female pronucleus, coming from the opposite direction, at a point near *k*. The segmentation nucleus passes on to the point *l* and divides in the direction of the anteroposterior axis of the egg, giving rise to the daughter nuclei *mm*. By subsequent divisions these give rise to the blastema nuclei, which migrate to the ventral and ventrolateral surfaces of the egg (*n*). It is by a tangential division of the blastema cells, forming a layer of much smaller cells, which creep around the sides of the egg and close on the dorsal surface, that the blastoderm is completed.

#### DORYPHORA.

Turning now to *Doryphora*, we find that the ovariole differs from that of *Blatta* in one particular: The terminal thread dilates below into a large oval chamber (*Endkammer*), the membranous wall of which is closely packed with cells of various sizes, containing nuclei which vary in size as the inclosing cytoplasm varies in volume. The nuclei contain delicate, much convoluted chromatin filaments. Besides the difference in size, no other differences are perceptible between the different cells.

At the lower end of the *Endkammer* the differentiation of the cells into ova and follicular epithelium takes place. Careful examination of many sections has convinced me that none of the peculiar phenomena described by Will (51) in the oögenesis of *Nepa* are to be observed in *Doryphora*. What I have seen is in perfect accord with Leydig's observations (29). The large cells of the *Endkammer* become the ova, and the smaller cells, after undergoing a further reduction in size by division, become the follicular epithelium.

In the two upper follicles the ova resemble in every respect the large cells of the terminal chamber, the nuclei retaining exactly the same perfectly spherical form, and the same distribution of their chromatin. In the ovum of the third follicle the chromatin

has assumed a different appearance. It is no longer distributed in the long, even, much convoluted filament, but has broken up into several spherules which stain more deeply. One or more large vacuoles are to be found in each one of these nucleoli, or masses of chromatin, which under a high power seem to hang suspended in the meshes of the nuclear reticulum in the same manner as the homologous bodies of *Blatta*. From the time of its first formation till the ovum has attained a considerable size, the follicular epithelium is columnar with its elongate nuclei directed at right angles to the long axis of the egg. Later the epithelium flattens, and the nuclei become kidney-shaped, with their long axes tangentially directed to the surface of the egg and their hili directed inwards.

The yolk first makes its appearance in the form of numerous granules. In no case have I seen a degeneration of the follicular epithelium to form yolk. The large granular yolk spheres soon make their appearance. As these bodies are much smaller than, but in other respects very similar to, those in *Blatta*, I have given little attention to their study. Though the protoplasm is reduced to a very delicate reticulum by the great accumulation of yolk spheres, there remains till the formation of the blastoderm, contrary to what I have observed in *Blatta*, a thick layer of finely and evenly granular protoplasm, which envelops the whole egg and is equivalent to Weismann's *Keimhaut*, though it is present from the first appearance of the yolk in the form of spheres, and does not originate just before the formation of the blastoderm, as in several of the insects studied by Weismann (47). The thick surface layer stains pale pink in borax carmine, and is quite distinctly marked off from the reticulate yolk-charged protoplasm of the interior of the egg.

After the nuclear filament has become metamorphosed into the spherical vacuolated masses above described, the nucleus moves from the centre of the egg to the surface, travelling along a line at right angles to the polar diameter of the egg. It thus reaches a point midway between the poles, taking the same position as the germinal vesicle of *Blatta*. During its migration the karyoplasm becomes amœboid, and except at its outer surface retains its irregular form even after taking its position right under the follicular epithelium. The outward directed face becomes excavated, the rest of its surface remaining con-



nected with intervittelline protoplasmic trabeculæ (Fig. 56 *tr*). The karyoplasm of the nucleus is coarsely granular. In the nucleus figured only two of the vacuolated masses of chromatin (or nucleoli, as most writers call them) are present. The larger contains six vacuoles, one of which incloses a bar-shaped mass of chromatin (Fig. 56 *nl*). In the cavity of the nucleus a number of more or less oval hyaline masses are seen. They are doubtless the equivalents of the "maturation spheres," noted above in *Blatta*. Stuhlmann (45) has found these same spheres in the degenerating germinal vesicle of *Lina*, a Chrysomelid allied to *Doryphora*.

The next stage found in the decomposition of the germinal vesicle is represented in Fig. 57. The karyoplasm has become confluent with the intervittelline protoplasm, and only the chromatin portion marks the spot where the nucleus reached the surface of the egg. The larger yolk spheres, formerly present even in the surface protoplasm, have passed inwards, and only the smaller spheres still remain in what is to become the blastema. Soon these, too, retire further into the egg, and the surface protoplasm is marked off from the vitelliferous portion. The remains of the nucleoli are worthy of attention. The vacuoles have disappeared, and the glistening chromatin has grown denser, and stains very deeply. In the case figured, one or two nucleoli have evidently broken into the nine fragments of different sizes and shapes. The larger and more peripheral mass (Fig. 57 *n*) is surrounded by a pale aureole. Its size, position, and the clear protoplasm surrounding it, seem to point it out as the important and permanent mass of chromatin soon to be converted into the first polar spindle. The remaining eight fragments seem to be leaving the surface and passing into the yolk, where they probably disappear, as no traces of them can be found in succeeding stages.

In Fig. 58, which represents the next stage in the nuclear metamorphosis, we find that the mass *n* of Fig. 57, which contained five spherical masses of dense chromatin, has become a perfect oval nucleus in the resting stage. The chromatin has again passed into the filamentous state. The surface layer of protoplasm is clearly developed and has secreted the vitelline membrane (Fig. 58 *v*). The chorion, too (Fig. 58 *ch*), has appeared. The follicular epithelium which secreted it is omitted in this and the next figures.

The resting nucleus just described soon begins to divide. Its small size prevents an accurate understanding of the peculiarities of its mode of division. Enough can be gleaned from Fig. 59, however, to show that the karyokinesis is not typical like that described by Flemming (12, 13) and Rabl (41) for the epithelial nuclei of *Salamandra*. No loops seem to be present in the metakinetic stage, but the chromatin is arranged in moniliform strings, each of which seems to be applied full length to one of the achromatic fibres of the spindle. I have not seen all the stages in the metakinetic process.

In the next stage observed (Fig. 60) the two masses of chromatin resulting from metakinesis have reached the poles of the spindle, where the fibres before apparent have become invisible. In the equatorial plane, however, the achromatic filaments are very distinct, being noticeably thickened. This thickening of the spindle fibres to form the dividing plate (*b*) between the two cells is of universal occurrence in plants, as may be seen from an examination of Strasburger's (44) delicate figures. It is, however, not infrequent in Arthropods. Carnoy (9) figures many instances in his "Cytodiérèse."

Unfortunately I have been unable, through lack of material, to trace the changes of the nucleus immediately following those just described. The ovum is deposited by the female *Doryphora* with its nucleus in the stage represented in Fig. 60 (compare *Blatta*). The outer mass of chromatin (*p*<sup>1</sup>) must be regarded as the first polar globule. Probably the process of forming the second polar globe is essentially the same as in *Blatta*.

Though incomplete, my observations prove, I think, that polar globules are also formed in the Coleoptera, thus adding another order of insects to the three in which these interesting bodies were found by Blochmann (5).

As in *Blatta*, the nuclei represented in Figs. 57 to 60 are very small and difficult to find in the enormously larger eggs.

Long before oviposition the eggs of *Doryphora* have acquired the dull orange color which makes them so conspicuous on the under surfaces of the leaves to which they are glued by the females. The coloring-matter is seated in the yolk bodies, and ultimately disappears in eggs preserved in 70 per cent alcohol. The eggs are most deeply colored in living specimens in the earlier stages, and a gradual fading of the color accompanies the

gradual metabolism of the deeply colored yolk into pale yellow protoplasm.

As the yolk spheres are much smaller in *Doryphora* than in *Blatta*, mutual pressure does not make them so clearly polygonal.

Though granular, the protoplasm, which is spread in such a thick layer over the surface of the yolk, contains none of the bacillar bodies so easily demonstrated in *Blatta*. It is of course possible that in the beetle's eggs they may be present, but of much smaller size and of spherical shape like those found in the *Lepidopteron Picris*.

The chorion in *Doryphora* is thick and somewhat leathery, though easily torn with the dissecting-needles. It seems to resemble in every way that of *Lina* as described by Graber (15). The surface layer of protoplasm secretes a very delicate and structureless vitelline membrane, which in the younger stages is closely applied to the surface of the egg. Soon after the formation of the ventral plate it is loosened and stands off from the surface. Besides some clear, irregular patches on the surface of the chorion I have seen no structures which could be interpreted as micropyles.

As there are strong reasons for supposing that the cleavage nucleus is situated in the very centre of the egg while dividing, the copulation of the pronuclei must take place along the radial line joining the centre of the egg to the point where the polar globules are formed. As I possessed no eggs immediately after oviposition, the phenomena of pronuclear conjugation, which could probably be more favorably studied in the eggs of *Doryphora* than in *Blatta*, on account of the perfect and even sections obtainable, were not observed.

The first stages after the one given in Fig. 60 which I have been able to find in my material showed the division immediately following the first and second divisions of the cleavage nucleus. As the few nuclei were all near the centre of the egg, and as Graber has found the cleavage nucleus is the centre of the very similar eggs of the allied *Lina*, I feel justified in believing that this is the point at which the first division occurs. The products of the cleavage nucleus go through karyokinesis, but owing to their much smaller size the process is much less distinct than in *Blatta*. In eggs stained with borax carmine, the cytoplasm of each cell appears as a delicate pink cloud among

the grayish yolk spheres, and very high powers are necessary to detect the delicate rays of the spindle or even the minute granules of chromatin in the metakinetic and succeeding stages.

The isochronism among all the nuclei in the different stages of development up to the formation of the blastoderm is quite as apparent as in *Blatta*. Judging from the great number of eggs with resting nuclei and the very few eggs with kinetic figures, I conclude that division takes place very rapidly and is followed by comparatively long periods of quiescence.

Fig. 61 represents one-half a cross-section through the equatorial region of an egg containing a number of nuclei in its yolk. All the nuclei are resting and are surrounded by amœboid masses of protoplasm. These cells often have the appearance of being in motion, most frequently in concentric paths. The nucleus is in the broader portion of the comet-shaped cell, which seems to be advancing head foremost. These cells are surrounded by numerous minute vacuoles that under the low power, with which Fig. 61 was drawn, appear like coarse granules.

These cells divide rapidly and give rise to many smaller cells scattered through the whole yolk. A few enter the blastema layer and begin to proliferate rapidly. As soon as this migration to the surface has taken place, the cells which have remained in the interior, and *which do not go to the surface*, stop dividing and take up positions at short but nearly equal distances apart, through the whole yolk. Before assuming their definite positions they have multiplied so rapidly that one may frequently see strings of three or four cells (Fig. 62 *yn*<sup>1</sup>). Often, too, in this stage most of the cells are in pairs, or, more accurately speaking, the egg contains many binucleate cells.

The nuclei which have entered the surface layer of protoplasm divide tangentially. Sometimes the axis of the spindle is inclined at an angle less than 90° to the radius of the circular cross-section, but in no case have I seen a spindle with its axis directed radially. The first divisions of the nuclei, which have entered the blastema, give rise to an even layer of cubical cells. By one more division of its constituent elements this blastema is converted into the blastoderm, which consists of smaller and more columnar cells. Sections taken in all directions through the egg show the blastoderm to be of even thickness over the whole surface (Fig. 63).



## GENERAL REMARKS.

*a. Nuclear Continuity.*

It will be seen from the above descriptive paragraphs, that I maintain that a portion of the chromatin of the insect egg *visibly* survives in the decomposition of the germinal vesicle and can be traced through the divisions resulting in the formation of the two polar globules into the cleavage nucleus and its descendants. This conclusion, which has always been held by careful investigators of the transparent ova of lower forms, has been seriously questioned of late by two workers, Stuhlmann (45) and Henking (20). The former, after investigating a number of Arthropod eggs in a superficial manner, comes to the conclusion that a stage exists in the ontogeny of the ovum when no traces of a nucleus can be demonstrated. Henking not only indorses this view, but describes in *Opilio* what are certainly the products of division of the cleavage nucleus as arising *de novo* in different parts of the egg.

As Blochmann (5) has pointed out the errors into which both investigators have fallen with far greater force than I can bring to bear on the subject, I will not increase the length of my paper by entering into a detailed account of their observations. Blochmann's beautiful researches on the early stages of the egg have proved beyond a doubt that the *Hexapoda* conform to the fecundative processes and method of polar-globule formation observed in other animals.

*That there is no moment when the nucleus ceases to exist as a nucleus* seems to me to be proved by my Fig. 11, where the remains of the nuclear wall are still present while the spindle is forming. True, the wall is absent in the younger stage, Fig. 10, and Fig. 11 may represent an exceptional case in which the wall has persisted longer than is usual, but it proves, nevertheless, that the matter composing the nucleus does not diffuse through the protoplasm and ultimately recombine to form the nuclei which give rise to the blastoderm, as Henking (20) would have us believe. The nuclear wall is known to persist in another Arthropod till after the commencement of spindle formation. I quote the following from the recent work of Weismann and Ischikawa (49): "Auch in den kleinen und dotterlosen

Eiern von *Bythostrephes* steigt das Keimbläschen bei Eintritt der Eireife in die Höhe, erblasst allmählich und zeigt zugleich an Eiern, die frisch in den Brutraum übergetreten sind, den Beginn der Spindelbildung *innerhalb* des dann noch scharf hervortretenden Umrisses des Keimbläschens."

The interesting researches of Weismann and Ischikawa (49), Leichmann's (28) recent discovery of two polar globules in *Asellus* and Pereyaslawzewa's (40) discovery of polar globules in *Gammarus pæcilurus* prove that the *Crustacea*, too, must be included under the general law.

#### b. *The Law of Orientation.*

Though considerable attention has been given to oökinesis in Echinoderms and Amphibia, no extended observations of these phenomena in the eggs of Arthropods have been published. In view of this fact, I have taken considerable pains to determine the paths of the pronuclei and cleavage nucleus in *Blatta*, and have devoted considerable space to their description.

A perusal of O. Hertwig's paper entitled, "Welchen Einfluss übt die Schwerkraft auf die Theilung thierischer Zellen?" (21), led me to try experiments to prove whether gravitation has any appreciable effects in determining the position of the embryo in the egg, or whether the position of the embryo with reference to the yolk is predetermined long before, during the development of the egg in the follicle.

It has been shown that the eggs of *Blatta* are carried in a horizontal position after the first day, so that the ventral or germinal faces of the upper row of eggs are directed downwards, and those of the lower row upwards. As the crista is continuous with the right side of the parent's body, the heads of the embryos all point to the right. It occurred to me that by keeping capsules in various positions any effects of gravitation on the development of the inclosed eggs could be easily determined. I accordingly placed capsules in five different positions on a block of paraffine provided with holes and grooves to keep them firmly in place. To prevent desiccation, the block was kept in a *camera humida*.

Capsules were kept from fourteen to twenty days in the following positions:—

1. Resting with the lateral faces perpendicular and crista uppermost.
2. Resting on the crista with the lateral faces perpendicular.
3. Resting on the left lateral face.
4. Resting perpendicularly on the anterior end.
5. Resting perpendicularly on the posterior end.

In all these cases the eggs developed normally, without the slightest indication of displacement in position or alteration of shape in the embryos; whether they were forced to develop with their heads pointing up or down.

The development was slow in all of the above cases, but this was not due to the unnatural positions of the capsules, but rather to the low temperature produced by the evaporation of the water under the bell-jar. That this was the true cause was shown by capsules kept under the same bell-jar in the normal position, on the right side. Their development was likewise retarded.

We may conclude from these few experiments that the force of gravitation has no perceptible effect on the development of the eggs of *Blatta*, but that these highly differentiated eggs, utterly unable to revolve in their envelopes like the eggs of birds and frogs, have their constituents prearranged, and the paths of their nuclei predetermined with reference to the parts of the embryo. As the only difference between the mature ovarian and the oöthecal egg is a difference in shape, we conclude that the predetermination is effected before fecundation, and even before the formation of the first polar globule.

There is nothing in the structure of the newly laid egg of *Doryphora* to prove that it possesses a dorso-ventral differentiation like the egg of *Blatta*; nor are my facts sufficient to warrant the assertion that the ventral plate develops on the side opposite the point at which the polar globules arise. Still the possibility of such a condition is in nowise precluded, and the observation of Blochmann and myself on *Blatta* probably apply to the Hexapoda in general. The spherical form of the Crustacean egg as opposed to the oval shape of the great majority of insect eggs, will be a great obstacle in the way of proving any similar conditions in this lower group.

It can be proved, however, that we have as true an anteroposterior differentiation in the eggs of *Doryphora* as in *Blatta*.

The eggs are deposited by the females in such a way that the pole which leaves the vagina first is glued to the surface of the leaf by a semifluid secretion, which at this point spreads out into a flat disc on which the egg rests and by which it is attached. As the hatching larva always leaves the egg head foremost at the opposite free pole of the egg, and as there is no revolution of the embryo as in Hemiptera, there can be no doubt as far as the cephalic and caudal ends are concerned that the relations of the embryo to the parts of the egg are the same as those described for *Blatta*. Moreover, the position of the eggs on the leaf and the position of the embryo in the egg, are sufficient evidence that the eggs are oriented in the ovaries of *Doryphora* with the cephalic pole directed towards the head of the mother insect.

Thus I have found that *Blatta* completely and *Doryphora* certainly in part conforms to the "loi de l'orientation de l'œuf" of Hallez (17), who found that the ova of *Hydrophilus* and *Locusta* lie in the ovaries with their cephalic ends directed towards the head of the mother insect, and that the dorsal and ventral surfaces of the egg are predetermined in the ovaries. Kadyi's (23) remarks make it certain that *Periplaneta* conforms to the law. In viviparous *Aphides* the same condition obtains, as may be gleaned from the plates of Metchnikow (30) and Will (52). When micropyles are developed at the cephalic pole of the egg, they form a fixed point which is of great assistance in observing whether the "law of orientation" obtains in a particular instance. We have such a case in *Corixa* as described by Metchnikow. In this insect (as also in *Aphis*), the entoblastic growth of the embryo somewhat obscures the process; but it can be readily seen that when the ventral plate forms, the portion of it which will subsequently grow out into the procephalic lobes is situated at the micropylar pole, which is anteriorly directed while in the body of the mother insect. The growing into the yolk of the embryo tail first brings the head to the opposite end of the egg, but during revolution the embryo regains the position which it held before the formation of the amnion and serosa (see Metchnikow (30), Plates XXVI. and XXVII. Figs. 6, 11, 20, 25, 27).



## THE FORMATION OF THE GERM LAYERS AND EMBRYONIC ENVELOPES.

*Doryphora.*

As my observations on the formation of the germ layers in the potato-beetle are both more copious and more satisfactory than in *Blatta*, and as *Doryphora* probably represents more nearly the typical process of germ layer formation, I will begin my remarks on this subject with *Doryphora*, and append what I have to say on *Blatta*.

The first change visible in the blastoderm from the surface is the appearance of a pair of folds which arise on the middle of what is to be the ventral surface of the egg (Fig. 66). The two folds may best be described as resembling a pair of but slightly bent parentheses close together. In cross-sections these folds are scarcely perceptible, and the difference in thickness between the ventral and dorsal blastoderm is very slight.

Soon the folds became more decided (Figs. 67 and 68), their anterior ends are continued around and meet so as to inclose a spade-shaped space, while their posterior ends diverge and are continued in the opposite direction to the caudal end of the egg, where the depression inclosed between the two folds turns inward and ends abruptly. The depression inclosed by the fold is to become the groove-shaped gastrula. The nuclei of the blastoderm now present a very different appearance from that represented in Fig. 66. The fold-surrounded depression at the anterior end (Fig. 67 *a*), lying where the stomodæum is subsequently invaginated, is apparently a differentiated portion of the gastrula, to judge from its peculiar shape. In lateral view (Fig. 68 *a*) this portion of the blastoderm is seen to be concave, the nuclei are closely aggregated, whereas anteriorly and posteriorly they are much scattered and have increased in size. The true distribution of the cells, as shown by their nuclei, is best seen in the lateral view of the same egg (Fig. 68). The aggregated mass of cells, or the ventral plate as it may now be called, is clearly marked off from the serosa or remaining blastoderm, which is recognized by its larger and more scattered nuclei. The ventral plate is seen to be constricted toward the middle of the egg to form two

lobes; the anterior broader and shorter is the procephalic, and the posterior and longer the abdomino-thoracic lobe. In both views of the egg (Figs. 67 and 68) a number of lines are seen crossing the ventral plate at right angles to the longer diameter. These lines make the plate appear segmented, and at first reminded me of Kowalevsky's figure (Plate VIII., Fig. 2), which represents an embryo *Hydrophilus* in exactly the same stage as that which I have figured. More careful examination, however, convinced me that the lines were not due to segmentation, nor, in fact, depressed at all, but were the wrinkles into which the ventral plate was thrown, probably by a contraction away from the anterior pole.

The simple method by which the ventral plate is formed is easily seen in a median cross-section of an egg in the stage figured in Fig. 67 (Fig. 64). The small projection *r* is the ridge which separates the thick and sinking gastrular portion of the blastoderm (*g*) from the remainder of the layer. As we have seen, all the cells of the completed blastoderm are columnar. The thickened ventral plate is formed merely by the cells on the ventral surface of the egg lengthening in a radial direction, and those of the dorsum (Fig. 64 *j*) changing their shape so as to have their long axes tangentially directed.

With further development the gastrular groove deepens and the ridges come close together in the median line (Fig. 70). The oral end of the gastrula (*a*) is oval, and is no longer marked off anteriorly by the ridge seen in Fig. 68. On each side of the oral widening is seen a small fold (*am*) between which and the gastrula the ventral plate cells are much thickened. This fold is the beginning of that portion of the amnion which subsequently envelopes the head, and the thickenings are probably the first traces of the brain. The egg (Fig. 70) viewed from the posterior end discloses some interesting facts (Fig. 69). The ventral plate has become pushed in at this point, and the thickened lip thus formed grows forward over it. This lip is the beginning of the caudal fold of the amnion and serosa. The gastrular invagination is considerably deeper at its posterior than at its oral end.

The caudal fold of the amnion and serosa grows much more rapidly than the cephalic folds. The tail end of the ventral plate advances dorsally till it is one-third the length of the egg

from the anterior pole. It pushes its way through the yolk in such a manner as not to bring the amnion or serosa in close apposition, but to inclose a greater or less amount of yolk between the two membranes. This dorsal growth of the caudal end shows considerable variation, however. In some eggs the end of the tail comes to lie at such a distance from the dorsal surface that it is almost in the centre of the yolk. In other instances the amnion and serosa become closely apposed and extrude the yolk from between them soon after the two envelopes have closed over the mouth, and the embryo has attained its maximum length.

In Fig. 71 I have represented the much curved embryo in this stage straightened out. The gastrular invagination has not yet closed, but it is much narrowed and more lengthened on account of the greater growth in length of the embryo. The oral end is still wider than the remaining portion. At the anal end (Fig. 71 *x*) the groove seems to bifurcate. At the point *x* the proctodæum is subsequently invaginated. Usually in embryos as old as that represented the anterior half of the gastrula has closed completely.

In the embryo figured the cephalic, maxillary, thoracic, and abdominal portions are already marked out. The first beginnings of the three pairs of legs are apparent in the undulating edge of the thoracic portion of the ventral plate ( $p^1 p^2 p^3$ ).

A median cross-section of the egg in the stage just described cuts the embryo at right angles to its long diameter in two places (Fig. 65). At the posterior end the thick amnion (*am*) is separated from the serosa by a layer of yolk (*y*), which will shortly be pushed out from either side to join the great central yolk mass. In this half of the section which is near the caudal end the gastrula is still open, though its cells have ceased to be columnar, and are dividing rapidly to form the thick lump of cells so very conspicuous at this point in slightly later stages. In the anterior portion of the egg the gastrula has closed, and the ectoderm and mesoderm are clearly separated. The tubular walls of the gastrula have broken down to form an irregular mass of polygonal cells which lie in the median line closely applied to the outwardly convex ectoderm. Though the closing of the gastrula progresses from before backwards, the closure of the oral portion is retarded and is marked by a

narrow oval pit which is visible till the mouth begins to invaginate (Fig. 73 *a*).

While the amnion and serosa are closing over the oral portion of the embryo the yolk begins to segment. The first traces of segmentation are visible on the dorsal surface between the end of the tail and the procephalic lobes. There the surface of the yolk assumes a scalloped appearance, and radially directed lines soon mark the divisions between the yolk balls. The segmentation progresses thence in a ventral direction, both from either side of the dorsum and directly inwards, so that finally the whole yolk is reduced to rounded masses, each of which contains from one to three vitellophags. Each yolk segment is properly a cell with its protoplasm radiating in all directions as a delicate reticulum which holds in its meshes the unequal-sized yolk spheres. By the time the amnion and serosa have completely formed, all the yolk has been converted into distinct subspherical segments, except the portions immediately under the anal and oral ends of the gastrula. Here the segmentation remains for a short time indistinct till the entoderm is established at these points.

In the embryo with completely closed envelopes (Fig. 73, Pl. V.) the procephalic lobes (*pcl*) have grown in size, and when attached to the egg clasp its upper pole. The three pairs of thoracic limbs are distinctly formed, while of the cephalic appendages only the 2d maxillæ (*mx 2*) are beginning to appear. The base of the attenuated ribbon-shaped abdomen shows traces of commencing segmentation. Posteriorly it suddenly widens out into a flat, transversely oval body, which I shall call the caudal plate. The gastrular invagination is closed except at its anal end (*x* 73), and the mouth will soon form at the shallow oval depression *a*, which marks the anterior end of the groove.

Fig. 82 represents a longitudinal section through an embryo a very little older than the one just described (Fig. 73).

The serosa (*sr*) now covers the entire egg, and is separated from the embryo proper and the amnion (*am*). Both membranes present the same appearance in section, being nodulated with nuclei. The anterior end of the embryo lies on the anterior end of the yolk in such a position that its mouth (*st*) is almost exactly at the pole; the tail ends somewhat anterior to the middle of the dorsal surface (*x*). The ectoderm, which at its cephalic



and caudal ends ( $\sigma$  and  $\rho$ ) passes imperceptibly into the much thinner amnion, is considerably thickened and has its crowded nuclei in several rows, though but one row of cells is present. The depressions which mark off the incipient appendages are deep and narrow. The mesoderm ( $msd$ ) is spread out under the whole of the ectoderm and has begun to thicken under each somite preparatory to segmentation. It is very noticeably thickened in two places: under the stomodæal depression ( $pl^1$ ) and under the caudal plate ( $pl^2$ ), where it forms a large mass of cells projecting into the as yet unsegmented yolk just beneath it. *These two masses of cells are the independent sources of the entoderm, which grows backwards as two strings from the anterior mass ( $pl^1$ ), and forward as two strings from the posterior mass ( $pl^2$ ). As we shall see further on, these two strings unite near the middle of the body and then begin to grow at their lateral edges till the mesenteron thus formed incloses the yolk.*

The points from which the chords grow are plainly seen in the figure ( $ent^1$  and  $ent^2$ ). Under both points of proliferation there are a number of nuclei which at first sight under a low power seem to be dividing karyokinetically. The chromatin is all aggregated in one or two dense masses in the hyaline karyochylema, and thus resembles the similar aggregations seen in kinetic nuclei. These nuclei, however, are not dividing, but undergoing decomposition, as we shall see when we come to examine a more highly magnified section through the caudal plate.

Before leaving Fig. 82 I would call attention to the three cells at  $c$  which are on the surface of the embryo in the amniotic cavity. They are very large and clear, and the more anterior is apparently creeping in the manner of an Amœba along the surface of the abdominal ectoderm. These cells, the ultimate fate of which I have been unable to determine, probably escape from the anal orifice of the gastrula before it closes. I have in several cases seen such cells issuing from or still in connection with the infolded pocket of ectoderm, which is called mesoderm as soon as the outer layer has closed over it (Fig. 87  $c$ ). These peculiar cells may be the homologues of the 'Polzellen' long ago observed in certain Diptera.

A much clearer understanding of the method of formation of the entoderm may be obtained from Figs. 87 and 88, both rep-

representing cross-sections through the middle of the caudal plate. In Fig. 87, from a younger embryo, the gastrula has not yet closed. Its walls are seen to be much thickened, and the karyokinetic figures show that its component cells are still proliferating. At the lower surface of the bag-shaped mass the cells are somewhat less compact and form a layer (*ent*) which at some points is separated from the superjacent cell-mass. This mass will give rise to the entoderm, and that above it to the mesoderm, as soon as the orifice *x* is definitely closed. *We thus have a mass of cells in which all three germ layers blend, and to no part of which can be assigned the name of a germ layer. Not till the groove is closed have we mesoderm, and not till the lower cells of the mass have become clearly differentiated from those above them can we speak of entoderm.*

The section Fig. 88 is from an embryo in which three germ layers are definitely formed, shortly after the closing of the gastrula. A depression (*x*) marks the point where the proctodæal invagination is to occur. The polygonal mesoderm cells are spread out in a mass (*msd*), which is separated by a more or less distinct line (*l*) from the entoderm beneath (*ent*). The differences between the cells of the last layer and the superjacent mesoderm are difficult to represent. Their nuclei are somewhat larger and clearer. They gradually merge into the mesoderm cells, the boundary being exceptionally clear in the section figured. Heider (19) says of these same entoderm cells in *Hydrophilus* that they are more "succulent" than the mesodermic elements. This adjective conveys the idea more clearly than paragraphs of description.

The peculiar nuclei which under a low power seemed to be dividing are now seen to be in a process of dissolution. *They originate in the entodermic mass and pass into the adjacent yolk, where they disappear*, sections through slightly later stages showing no traces of them. From what I have seen I believe these nuclei to pass through the following stages, examples of all of which may be found in a single embryo. The karyochylerema becomes vacuolated, probably with substances absorbed from without, to judge from the large size of some of these nuclei (Fig. 88 *v*), while the chromatin ceases to present the threadlike coil and becomes compacted into irregular masses between the vacuoles. Finally, the vacuoles fuse and the masses of

chromatin, formerly numerous, agglomerate to form one or two large irregular masses which usually apply themselves to the wall of the clearly vesicular nucleus (Fig. 88 *t*). The wall of the nucleus then ceases to be evenly spherical, and becomes irregular apparently because the karyochylema is escaping through a rent (Fig. 88 *o*). In the last stages seen the masses of chromatin lie between the yolk bodies, all the other portions of the nucleus having disappeared. They still take the characteristic deep red stain, but finally become comminuted and disappear in the intervittelline protoplasm.

The dissolution of these nuclei and their migration into the yolk is brought to a close soon after the entodermic mass begins to grow forward.

The oral mass of proliferating cells is essentially the same as the caudal mass just described; but being smaller, I have not seen fit to represent it in the plates by enlarged figures. Some of the entoderm nuclei degenerate in exactly the same manner as those described in the caudal thickening, but the whole mass of cells being smaller, the number of these evanescent nuclei is much less.

I am at a loss to assign a meaning to this migration of degenerating entoderm nuclei into the yolk unless it be supposed that originally all the nuclei of the egg went to the surface and that a portion of the entoderm passed into the yolk to form vitellophags while another portion proliferated forward in compact sheets to form the walls of the mesenteron. Later, when the ontogeny was abbreviated in the blastoderm stage by cells being left in the yolk, this migration of entoderm cells became unnecessary, as the yolk, which is already segmented, is copiously supplied with vitellophags. The lack of distinct yolk segmentation just beneath the two proliferating points may lend some probability to this view. I am aware that my explanation halts, but it will have to stand, for the want of a better one, till more facts are forthcoming on these degenerating nuclei in other forms.

In examining the literature the only observation which I can find similar to the one just recorded is in Hatschek's paper on *Bombyx chrysorrhæa* (18). He observed a mass of nuclei, which in his figures have all the appearance of undergoing degeneration, just anterior to the large mass of entoderm cells attached to the oral ectoderm. This mass of nuclei, designated by him as a "gland," soon disappears in the yolk.

*Blatta.*

My observations on the formation of the germ layers in *Blatta* are less satisfactory than those on the same process in *Doryphora*, because the eggs of the former are difficult to section and have small, indistinct cells in the later stages. I have, however, given much attention to the subject, sufficient, I believe, to be able to assert that the method of germ layer formation departs from the type observed in *Hydrophilus* and *Doryphora*.

As soon as the blastoderm is completed by the rapid proliferation of the blastema cells, the whole layer of protoplasm with its embedded nuclei contracts from the lateral faces towards the front of the egg. The blastoderm thus becomes exceedingly thin on the lateral and dorsal surfaces of the egg, and the nuclei of these surfaces become much scattered and flattened, while the protoplasm is thickened on the whole ventral face, where the nuclei are crowded together and have again become spherical. A slight further contraction away from the cephalic and caudal ends towards the centre of the ventral face shortens this mass of thickened cells into the ventral plate.

While the blastoderm is thickening, nuclei are being given off centripetally to form the yolk cells. A few of these nuclei go deep into the yolk, but the great majority remain at or very near the surface. They are not given off in a continuous sheet, nor are they produced from the blastoderm by any invagination. They are simply nuclei which have been sent into the yolk from different and often widely separated points of the contracting blastoderm. The few nuclei which descend into the yolk remain for a long time small and indifferent. Sometimes the number of these nuclei is very limited so that they occur in only a few of a great number of complete longitudinal sections passed through an egg.

The nuclei of the surface yolk undergo considerable differentiation, and are soon easily distinguished from the superjacent blastoderm. They surround themselves with stellate cytoplasm, retain their spherical or spheroidal shape, and often present one or more large nucleoli (Figs. 29 and 32 *v*). Their function for many days is the conversion of the yolk into soluble compounds to be absorbed by the rapidly dividing cells of the embryo. During this process they grow rapidly, and soon become the



largest cells with the largest nuclei in the egg (Fig. 30 *v*). The long pseudopodial continuations of the finely and evenly granular cytoplasm can often be traced for a considerable distance between the yolk polyhedra. The yolk cells are never seen in process of division, and as their number in eggs of widely different stages is approximately constant, I conclude that they rarely or never divide.

The thickening process which formed the ventral plate still continues in a spot about one-fourth the length of the egg from the caudal end, and gives rise to a rounded mass of cells which are much thicker than the surrounding portion of the ventral plate though but slightly raised above the general surface (Fig. 41). A faint depression appears in the centre of the rounded mass (*bp*). While this thickening is forming, the nuclei of the ventral plate are also proliferating very rapidly at two points on the ventrolateral edges about one-fourth the length of the egg from the cephalic end (Fig. 41 *pcl*). These cells also increase in depth, but do not rise above the general surface of the egg. The two patches of thickened cells are the precursors of the procephalic lobes. The deceptive appearance of a groove is presented by the keel (*cn*), which runs the whole length of the ventral face, but soon disappears as it is absorbed by the young embryo.

The formation of the mesoderm can be traced in eggs sectioned during or shortly before the stage figured in Fig. 41. Figure 38 is a longitudinal section through the posterior portion of the egg (Fig. 41) through the middle of the thickened mass of cells and the depression *bp*. In this egg the mesoderm has been forming for some time. The ventral-plate cells are columnar at *bp*, and their nuclei are elongated in just the opposite direction to their former longest axis, which is still the longest axis of the serosa nuclei at *sr*. The depth of the ventral-plate cells gradually decreases anteriorly. The stellate yolk cells are scattered at various distances from one another under the ventral plate. The mesoderm (*msd*), as is clearly seen from the section, arises partly from proliferation of the ventral-plate cells under *bp* and passes forward as a single but incomplete layer of cells. Towards the head this layer splits, and each of the two bands thus formed continues forwards under one of the procephalic thickenings. This is seen in Fig. 31 from a sec-

tion through the point *pcl* of the egg represented in Fig. 41. *ecd* is the thickened ectoderm, *msd* the mesoderm, which is absent in the middle of the ventral face at *c*.

That the mesoderm grows forward from the rounded caudal thickening may be proved by sections through a number of eggs taken from capsules six and one-half to eight days old. The eggs will be found in various stages more or less close to that given in Fig. 41. In some a very short row of mesoderm cells is found just in front of the thickening; in others the row will be longer as it has advanced further to the cephalic end. Only part of the mesoderm is formed at the thickening. As can be concluded from the even arrangement of the two layers anterior to *bp* in Fig. 38, each ectoderm cell has a mesoderm cell beneath it, showing that the mesoderm is derived from the ectoderm by centripetal division. The impulse to this division, however, seems to originate in the incomplete invagination at *bp* and to travel towards the head of the embryo.

After the mesoderm is formed, the depression *bp* disappears, and the amnion and serosa begin to develop. They rise as a crescentic fold from the rounded posterior edge of the area of proliferation (Fig. 42 *as*). The cells of the procephalic lobes become more prominent, and while the caudal fold of the amnion and serosa is growing in length and continuing up the edge of the ventral plate, a fold also arises from the outer edge of each procephalic area and bends inward. This stage in the development of these membranes is seen in Fig. 43.

The embryo is now slipper-shaped, the toe of the slipper being the caudal and the heel the cephalic end. The growth of the membranes continues, the toe of the slipper completing itself more rapidly than the heel. Soon the two procephalic folds are connected around the anterior tip of the ventral plate, which is undergoing a change in outline. Figure 44 shows the amnion and serosa almost closed. Over the spot where the stomodæal invagination will soon appear, there is still a small, slit-shaped opening in the membranes, but this soon closes; not, however, till after the appendages, both cephalic and thoracic, have begun to appear.

The structure and formation of the amnion and serosa, as well as their relations to each other, can be made out from the sections (Figs. 29, 30, and 32). Figure 29 is a transverse section

through the point *c* of Fig. 43, a region at which the two folds have not yet arisen. The ectoderm (*ecd*) is very thick, especially in the median ventral line. The mesoderm (*msd*) is incompletely separated from the ectoderm, and is seen only in the median portion of the section. The yolk cells are large and distinct. Their chromatin forms large nucleoli. The yolk under the embryo is becoming much vacuolated.

The section (Fig. 32) passes through a point a little in front of *as* in Fig. 43. This embryo was older than the one represented in Fig. 42; hence the yolk cell (*v*) is much larger and the mesoderm more distinctly separated from the ectoderm. The infolding of the ectoderm to form the amnion and serosa is seen on either side. The amnion (*am*) is thicker than the serosa (*sr*). Its nuclei are small, close together, and spherical, while the nuclei of the serosa are large, flat, and scattered. Figure 30 is a section through a point near *c*<sup>1</sup> (Fig. 43), of a slightly older embryo. The amnion and serosa are completed and in close contact with each other, so that the yolk cannot pass in between them. The difference between the nuclei of the amnion and serosa is very pronounced. The mesoderm (*msd*), which is several cells deep, and is now distinctly separated from the ectoderm, has become an independent layer. Its nuclei are more spherical than the ectoderm nuclei, many of which are considerably elongated and flattened.

The entoderm is formed very late in *Blatta* (about the 15th or 16th day), and in cross-sections of embryos of that age it may be seen as a thin layer of cells on either side of the ventral yolk closely applied to the inner face of the splanchnic mesoderm (Fig. 54 *ent*). Cholodkovsky (10) claims that these bands of entoderm are derived from the splanchnic mesoderm by delamination, but an examination of a number of sections has convinced me that it is next to impossible to come to any definite conclusion as to the mode of origin of the entoderm in *Blatta*. By the time it has begun to form the cells have become very minute, and different tissues of very different origins have become closely united, so that the proximity of splanchnic mesoderm and entoderm is no proof of the derivation of the latter from the former. I have been able to satisfy myself, however, that the entoderm appears in two thin layers, one on each side of the median ventral yolk, and that these two layers converge

anteriorly and posteriorly, and become united to the inner ends of the stomodæal and proctodæal pockets, in a manner which differs in no respect from what is observed in *Doryphora* after the entoderm has become definitely established. I can therefore see no reason for adopting Cholodkovsky's view as proving that the entoderm arises in a manner differing from that described above for *Doryphora*. As far as *Blatta* is concerned the question of the formation of the inmost germ layer must still be regarded as an open one.

The embryo is hammer-shaped when the amnion and serosa have closed. The cephalic lobes extend around on to the lateral surfaces of the yolk, and each soon becomes divided into two lobes, a larger anterior and a smaller posterior one (Fig. 44). The posterior lobe is the commencement of the antenna (*at*). In many embryos one, or, more rarely, both antennary lobes are temporarily bilobed (Fig. 44). This may be a slight reversion, tending to show that the antennary lobes originally gave rise to two pairs of appendages which were perhaps homologous with the two pairs of antennæ in the Crustacea. The mandibles and first and second maxillæ are just visible as faint outgrowths of the ectoderm, while the more pronounced three pairs of thoracic legs have produced a widening of the embryo in the middle of its length (Fig. 44 *p*).

The time required for the development described in the preceding paragraphs is about four days. The blastoderm begins to contract and thicken on the seventh day from the commencement of development, and by the end of this day the area of proliferation is formed. Early on the eighth day the amnion and serosa begin to appear. They develop rapidly, so that the embryo is in the slipper stage by the close of the eighth day. The amnion and serosa are almost or quite closed by the end of the ninth day. During the tenth day the mesoderm is segmented, and the cephalic and thoracic appendages begin to appear. The embryonal envelopes are completely formed by the end of the tenth day, and the embryo has assumed the shape of a hammer or mallet.



## GENERAL REMARKS.

*a. Germ layers.*

Our knowledge of the formation of the germ layers in the Orthoptera is still less satisfactory than in other orders of insects, as in most of the species studied even the formation of the mesoderm has not been clearly determined.

Korotneff (25) failed to find the typical groove-shaped gastrula in *Gryllotalpa*, and Ayers (1) had no better success with *Æcanthus*. On the other hand, Bruce (7) has observed the typical process of mesoderm formation in *Mantis*, and Graber (15) in *Mantis* and *Stenobothrus*. Thus only representatives of the Orthopteran families *Mantidæ* and *Acridiidæ* are known to form their mesoderm in the typical manner.

Nusbaum (33) concludes, on apparently very little evidence, that the mesoderm of *Blatta* is formed in the same manner as in *Musca*, and he gives a figure of a cross-section with an immense invagination.

Cholodkovsky (10), in his account of the entoderm formation in *Blatta*, says that the gastrula which gives rise to the inner layer is very easily observed.

As, I spent much time on a full series of stages between the formation of the ventral plate and the appearance of the appendages, without being able to find a trace of the elongate gastrula for which I was searching, I conclude that both Nusbaum and Cholodkovsky may have been deceived by the carina on the ventral surface, which, in reflected light, looks like a narrow groove.

The method of germ-layer formation in *Blatta*, at first sight so different from the method observed in *Doryphora*, may, however, be traced to the typical process. My studies on *Doryphora* make it probable that the entoderm of *Blatta* originates in the mass of cells found under the area of proliferation, the more superficial cells of which grow forward as the mesoderm in a continuous median sheet bifurcating under the cephalic portion of the ventral plate. We should thus have a spot differing in no essential particular from the caudal plate of *Doryphora*. If we suppose that in *Blatta* the tendency to form the median groove has become very weak, and is now confined to

the posterior end of the ventral plate, we may regard the depression *bp* as the remains of the blastopore. I have remarked that the gastrula in *Doryphora* is much deeper posteriorly than anteriorly, and providing a tendency to obliterate the invagination should become apparent in an equal degree throughout its whole length, a short posterior depression like that in *Blatta* would be the result. But the opposite possibility, viz.: the derivation of a gastrula like that of *Doryphora* from a circular form like that of *Blatta*, is likewise worthy of attention. According to Sedgwick (43), the gastrula of *Peripatus* elongates with a concomitant closure of the median portion of its orifice. Of the two openings thus formed the anterior becomes the mouth while the posterior becomes the anus of the embryo. Providing a similar stretching of the gastrula has taken place in the ancestors of *Doryphora* and *Hydrophilus*, it would be easy to see how the cells of the original single *Entodermanlage* might be separated to form two masses, which now arise beneath the stomodæal and proctodæal area, and how the formation of the mesoderm from the edge of what was once the gastrula lips might continue throughout the whole portion of the embryo between the mouth and anus. If this has been the true evolutionary process in the development of the elongate gastrula of insects, it seems probable that *Blatta* may represent

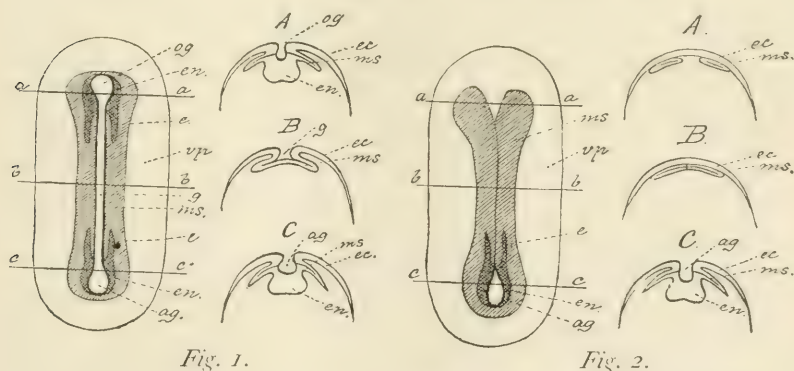


Figure 1.—Diagram of germ-layer formation in *Doryphora*. *vp*, ventral plate; *ag*, oral end of gastrula; *ag*, anal end of gastrula; *g*, central portion of gastrula; *en*, entoderm; *e*, prolongations of entoderm; *aa*, plane of cross-section A; *bb*, of cross-section B; *cc*, of cross-section C; *ec*, ectoderm of ventral plate; *ms*, mesoderm.

Figure 2.—Diagram of germ layer formation in *Blatta* (somewhat hypothetical). Letters the same as in Figure 1.

the more primitive and *Doryphora* the more modified method of germ-layer formation. I would note in this connection that the mesoderm of *Blatta* is formed in a manner strikingly similar to that observed in *Peripatus* by Kennel (24). Reference to the diagrams, Figs. 1 and 2, will make further remarks on the relation of the two modes of germ-layer formation in *Blatta* and *Doryphora* unnecessary.

Kowalevsky, Hatschek, Patten, Heider, and Bütschli have published observations which have a decided bearing on the method of entoderm formation in *Doryphora*.

Kowalevsky (26) claimed in his epoch-making work that in *Hydrophilus* the two longitudinal bands of entoderm are derived by delamination from the splanchnic mesoderm, which he erroneously supposed to originate from the primitive mesodermic layer by an incurling of its lateral edges. As we have seen, Cholodkovsky also claims that the entoderm of *Blatta* is derived by delamination from the splanchnic mesoderm.

Hatschek (18) figures in *Bombyx chrysorrhæa* a large mass of entoderm cells immediately beneath the stomodæum. This mass may be compared with either the anterior or posterior cell masses of a similar nature in *Doryphora*.

Patten (38) figures a cluster of several huge entoderm cells attached to the stomodæum of *Neophalax* (Pl. XXIV. C. Fig. 36), and in a more recent paper (39) he has figured similar cells in the same position in the embryo *Acilius*.

Two recent papers on *Musca*, one by Kowalevsky (27) and one by Bütschli (8), contain accounts of a method of entoderm formation very similar to that observed by me in *Doryphora*.

Kowalevsky finds that the entoderm originates in two widely different points, anteriorly at the inner end of the stomodæum and posteriorly at the inner end of the proctodæum, from some of the cells of the gastrular invagination. The mass of entoderm at either of these places forms a watch-glass-shaped body with its concavity applied to the yolk. From the lateral edges of each mass the entoderm cells proliferate to form two bands, each of which unites with the one on the same side growing from the opposite direction. By a dorsal and ventral growth of the edges of the two bands the entoderm envelops the yolk and thus completes the mesenteron. Kowalevsky also regards the entodermic invagination in insects as a greatly elongated gas-

trula, which has retained its ability to form entoderm only at the oral and anal ends. Putting this construction on the gastrula, it is, of course, easy to reduce the germ layers of insects to the *Sagitta* pattern.

Kowalevsky's results on *Musca* have been corroborated as far as the posterior *Entodermanlage* is concerned by Bütschli (8); while his main results on *Hydrophilus* have been confirmed by Heider (19).

According to Heider, the tube formed by the closing gastrula flattens out, and the half of it immediately below the ectoderm becomes mesoderm, afterwards splitting into the somatic and splanchnic layers; while the other (inner) half becomes the entoderm which spreads apart to form two bands, one on each side applied to the part of the mesoderm inclosing the coelomic cavity. Subsequently the proliferating edges of the bands unite ventrally and dorsally to complete the mesenteron.

A comparison of my account of *Doryphora* with Heider's account of *Hydrophilus* will show that I differ from Heider on one point only. I claim that all the entoderm between the oral and caudal widenings of the blastopore is not derived from the inner cells of the gastrular depression, but grows in from the ends of the body. I do not deny that the entoderm may arise in *Hydrophilus* (and possibly in *Doryphora*) in the manner described by Heider, *i.e.* from the inner layer of cells of the gastrular tube when it flattens out and breaks down, but I would regard the process as confined to two very small areas, one being stomodæal, the other protodæal.

Heider's figures are undoubtedly correct and correspond in every way to sections through *Doryphora* embryos in corresponding stages. Unfortunately, he has not noted with any precision the plane of section of the different preparations figured. Starting with his Plate II., his figures may be interpreted in harmony with *Doryphora*, thus:—

Figure 23 is exactly like my Fig. 88, omitting the degenerating nuclei, and I should interpret it in the same way as Heider. My section passes through the caudal plate of the embryo; Heider's passes "durch den Abdominaltheil," which is indefinite. In Figs. 24 and 25 I can see no entoderm, but merely the apposed splanchnic and somatic layers of mesoderm between the lateral ends of which the coelomic cavities are about to



form, these cavities being simply enlargements of the at first very limited space between the two layers at their outer extremities. Figure 25 is a section through the "Abdominaltheil."

Both figures accurately represent cross-sections through the middle of the ventral half of the egg of *Doryphora* before the proliferating bands of entoderm have reached the plane of section (compare my Fig. 78). Heider's Fig. 26 just skims the ends of the proliferating bands, showing four entoderm cells at *i* beneath the left cœlomic cavity in the figure. No portion of the band was cut on the opposite side, as either the section was slightly oblique or one of the bands had grown somewhat more rapidly than the other, a condition which I have often observed in *Doryphora*.

The most definite proof that *Hydrophilus* does not differ from *Doryphora* is to be gained from Heider's own words. He says: "Wir müssen aber nun auf ein höchst merkwürdiges Verhalten eingehen, welches uns beweist, bis zu welchem Grade coenogenetische Veränderungen den ursprünglichen Typus der Insectenentwicklung entstellen. Während nämlich die geschilderte Abtrennung des Entoderms von dem unteren Blatte Kowalevsky's im vorderen Theil des *Hydrophilus*-Embryos (den Kopf- und Thoraxsegmenten) deutlich zu beobachten ist und ebenso klar in den letzten Abdominalsegmenten zur Ausbildung kommt, treffen wir entsprechend den vorderen Segmenten des Abdomens eine Querzone des Embryos, in welcher keine Entodermchicht zur Anlage kommt — mit anderen Worten: die Entodermanlage entwickelt sich im Vordertheil und nahe dem Hinterende des Embryos in zwei gesonderten Stücken, welche erst in späteren Stadien gegeneinander wachsen und mit einander verschmelzen. Diese gesonderte Ausbildung des Entoderms vom Vorder und Hinterende des Embryos ist ein Seitenstück zu dem von uns geschilderten und (Taf. L. Fig. 4) abgebildeten, selbständigen Auftreten des Vorder- und Hinterendes der rinnenförmigen Einstülpung. Wie ich aus den Angaben Kowalevsky's and Grassi's ersehe, weist das Darmdrüsenblatt der Biene hinsichtlich seiner ersten Anlage ähnliche Verhältnisse auf."

#### *b. Embryonic Envelopes.*

No phenomenon in the development of the insect embryo is better suited to call forth conjecture than the embryonic enve-

lopes and the dorsal organ formed soon after their rupture. For the sake of clearness I shall here consider only the envelopes and relegate the discussion of the dorsal organ to my remarks on the revolution of *Blatta* and *Doryphora* at the end of the next descriptive division of my subject.

Various theories, all more or less vague and intangible, have been advanced by different investigators to account for the amnion and serosa. Balfour (2) regarded these membranes as possibly derived from an early ecdysis. Ayers (1) refuted Balfour's suggestion; but as he started out in his own explanation with incorrect suppositions regarding the homologies of the different germ-layers in insects with those of other animals, he could not fail to involve the amnion and serosa in the general error. Kennel (24) regards the embryonic membranes of insects as homologous with the so-called "amnion" in *Peripatus*, and both structures as the remains of the trochosphere of the annelid ancestor. Emery (11) suggests that the envelopes may be homologous with the shell of the Entomostraca.

The question as to the meaning of the envelopes in insects has been greatly confused by drawing in the widely different envelopes of *Peripatus*, Scorpions and Myriopods and the Crustacean dorsal organ, presenting all the different forms observed in *Oniscus*, *Asellus*, *Cymothoa*, *Mysis*, etc. Some authors agree with Kennel in regarding the embryonic envelopes throughout the Arthropoda as homologues. According to others the dorsal organs of the Crustacea are the homologues of the amnion and serosa of hexapods. Still others maintain that the Crustacean dorsal organ is to be brought into connection with the occasionally similar dorsal organ of insects.

Will (52) has of late advanced a theory to account for the formation of the embryonic envelopes of insects only. His theory has the advantage over its precursors in that it replaces such indefinite terms as "early ecdysis," "shell of the Entomostraca," and "Trochosphere" by facts derived from the comparative morphology of the membranes themselves. As I came to essentially the same conclusions as Will long before reading his article, I may be pardoned for presenting the subject in my own words, though they repeat in great measure what has appeared in Will's paper.

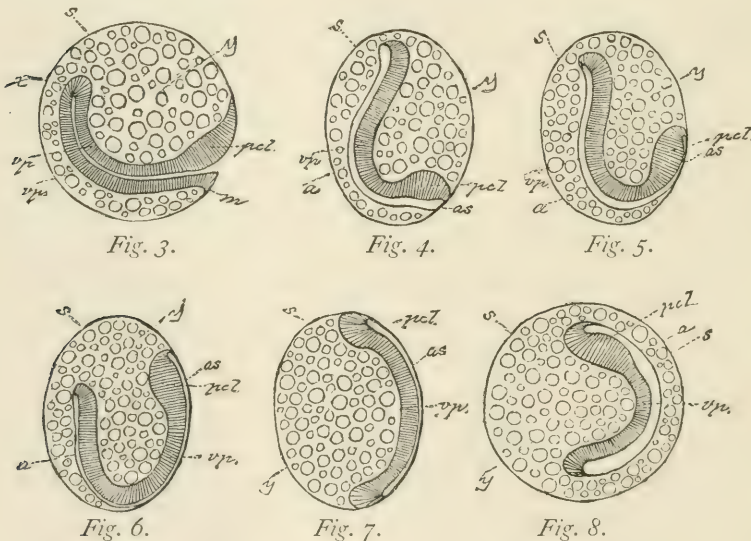
The problem as to the meaning of the amnion and serosa is restricted to the Hexapoda by postulating the following:—

1. There are no sufficient reasons for homologizing the embryonic envelopes of insects with the homonymous but dissimilar structures in Myriopods, Scorpions, and *Peripatus*.

2. There is no more than a superficial resemblance to speak for an homology between the dorsal organs of the Crustacea and the embryonic envelopes of Insects or between the dorsal organs of Crustacea and the homonymous structures in Insects.

3. The dorsal organ of insects may be regarded as the necessary result of the rupture and absorption of the embryonic envelopes, and consequently as in no way related to such structures as the dorsal organs of *Cymothoa*, *Limulus*, etc.

The process of envelope formation has been observed in numerous insects of all orders with sufficient accuracy to warrant the assertion that all the pronounced types are connected by intermediate forms in fine gradation; a fact which was long ago expressed by Kowalevsky (26).



Diagrammatic longitudinal sections of embryos just after the completion of the envelopes. Figure 3, *Geophilus*; Figure 4, *Calopteryx*; Figure 5, *Aphis*; Figure 6, *Doryphora*; Figure 7, *Blatta*; Figure 8, *Bombyx*. a. amnion; s. serosa; as. amnion and serosa apposed; vp. ventral plate; pcl. procephalic lobes; y. yolk.

If we suppose such a form as *Calopteryx* to present the original mode of embryo formation in the Hexapoda (and Paleontol-

ogy makes such a supposition probable), we have a form which will unite readily with an embryo Myriopod in a corresponding stage of development. In Fig. 3 I have given a diagrammatic longitudinal section of *Geophilus* about the time the appendages appear. Evidently either the excessive growth in length of the annelid-like body has necessitated the complete invagination of the embryo into the yolk, bringing the caudal and cephalic ends together, or this process has been adopted as a means of bringing the surface of the embryo into more complete contact with the yolk. It is only necessary to reduce the posterior half of the infolded embryo (included between  $x$  and  $m$  in the figure) to a thin membrane to reach the condition of *Calopteryx* (Fig. 4). The membrane resulting from the attenuation would be the amnion. Will has emphasized the fact that the stage with the amnion almost as thick as the ventral plate with which it is continuous, still occurs in the ontogeny of insects (compare *Blatta* and *Neophalax*). He suggests that the attenuation of the posterior half of an embryo like *Geophilus* to form the amnion may account for the great disparity in the number of segments between the Hexapoda and Myriopoda.

A further difference is observable between *Calopteryx* and *Geophilus*. The end of the original caudal extremity in the former is joined to the anterior end of the ventral plate, thus closing the sack whose anterior wall is the ventral plate and whose posterior wall is the amnion. This sack is attached at one point to the serosa enveloping the egg. The union of the membranes to close completely the amniotic cavity is the hinge about which the further explanation turns.

It seems essential in all the insects so far studied excepting *Musca*, where the envelopes are rudimentary, that the amniotic cavity should be shut off from the space between the vitelline membrane and the surface of the yolk. The reason for the closure is apparent if we regard the amniotic cavity as a place for the temporary deposition of excreted matters, as an organ functionally analogous to the allantois of higher animals. It has often been observed that the amniotic cavity of insects soon after its formation becomes filled with a clear liquid which during and after revolution is found as a much vacuolated coagulum about the feet of hardened embryos. It seems probable that while the inner ends of the ventral-plate cells are absorbing and



metabolizing the yolk, their outer ends are at the same time giving off into the amniotic cavity a less amount of liquid waste products. Providing this supposition is true, we should have a sufficient reason for the constant closure of the amniotic cavity.

We have a complete series of finely graduated forms of envelope formation from the method observed in *Calopteryx* (Fig. 4) to *Blatta* (Fig. 7). *Aphis* represents the first step in the transition of an *entoblastic* embryo like *Calopteryx* to the decidedly *ectoblastic* form seen in *Blatta*. This transition consists in leaving more and more of the anterior end of the embryo on the surface of the yolk. In *Aphis* (Fig. 5) the whole head is left outside the invagination; in *Doryphora*, the head and the anterior half of the body. When a portion of the embryo is left on the surface, the closure of the amniotic cavity necessitates a backward growth of the angle formed by the fore end of the head and the abutting serosa (*as*, Fig. 5) to form a fold which unites with a similar fold formed at the opposite end of the embryo. In *Doryphora*, where much of the embryo lies on the surface of the yolk, the posterior or caudal fold of the amnion and serosa has to grow forward a considerable distance to meet the cephalic fold. *Blatta* has advanced still further than *Doryphora*. The embryo no longer grows into the yolk, but the formation and ultimate closing of the membranes continues.

At first sight it would seem more natural to suppose that the result attained in *Blatta* was brought about simply by an extrusion of the yolk between the amnion and serosa of such a form as *Aphis* or *Calopteryx*, but the law of orientation, as explained in a preceding paragraph, forbids such an interpretation. The head of the *Aphis* embryo is at the time of the completion of the membranes close to the spot before occupied by the caudal end of the ventral plate, and after revolution the caudal end of the embryo will again be located at this end of the egg. Hence the typical *ectoblastic* originated from the typical *entoblastic* embryo, not by an extrusion of the yolk from between the amnion and serosa, but by a gradual weakening of the invaginative process. The weakening, of course, results in more and more of the anterior portion of the ventral plate remaining inert, though the growth of the membranes to shut off the amniotic cavity continues.

The peculiar free *entoblastic* embryo observed in *Lepidoptera*

(Fig. 8) may have originated in two ways: either from a suspended entoblastic embryo like *Calopteryx* by a separation of the amnion from the serosa at the point of suspension (Fig. 4 *as*) and the consequent passage of yolk between the two membranes, or from the ectoblastic type of *Blatta* by a separation of the amnion from the serosa throughout their area of contact, accompanied by an intrusion of yolk. All that we at present know concerning the formation of the envelopes in Lepidoptera tends to prove that the latter method is the more probable.

The hypothesis of Will and myself as set forth in the above paragraphs might be called a *mechanical* explanation as opposed to the views of those who see in the embryonic membranes rudimental structures like the remains of the trocosphere, larval skins, etc. Our hypothesis has at least the virtue of utilizing the facts near at hand.

#### DESCRIPTION OF THE EXTERNAL CHANGES IN THE EMBRYO BLATTA AND DORYPHORA UP TO THE TIME OF HATCHING.

##### *Blatta.*

Soon after their completion, the amnion and serosa become more attenuated on account of the flattening of their cells and the consequent diastasis of their nuclei. This thinning out of the envelopes permits a better view of the embryo and its forming appendages.

On about the tenth or eleventh day from the beginning of development, the embryo presents the appearance represented in Fig. 45. The broadly rounded procephalic lobes are separated by a deep incision in the median line, and the antennæ (*at*) growing from the posterior lateral corners of the lobes have become prominent, while the backward direction of their growth is apparent. The labrum (*lb*) has appeared as a thick, crescentic and slightly divided fold in front of a faint depression which is the commencement of the stomodæal invagination. Of the three pairs of oral appendages, the second and third (*mx*<sup>1</sup>, *mx*<sup>2</sup>) are clearly rounded and directed backwards; the mandibles are still small. Each segment of the abdomen presents a pair of indistinct appendages. These subsequently disappear, with the exception of the pairs on the basal and terminal segments, which undergo a differentiation peculiar to themselves. As I

have given elsewhere (50) a minute account of the pair of appendages belonging to the first abdominal segment, I shall not consider them in the present paper. The pair of appendages belonging to the terminal segment persist and become the anal stylets. Unlike most Arthropod embryos, the caudal end of the embryo *Blatta (cpl)* is never bent dorsally, but from the very early stage in which it is in a line with the long axis of the abdomen, shows only a ventral flexure. Owing to this flexure, which soon becomes very pronounced, the formation of the protodæum cannot be as easily observed as in *Doryphora*.

The changes which are apparent in surface views by the fourteenth or fifteenth day have been carefully represented in Figs. 46 and 47. In the former the embryo is *in situ* on the yolk, in the latter it is isolated and seen from the ventral surface.

As may be indistinctly seen in Fig. 47, the first and second maxillary appendages have each become split up into three divisions. In *Ecanthus*, according to Ayers, "the three oral appendages are trilobed; the lobation is most prominent in the second maxillary, and least in the mandibular appendages. The primitive appendage is first divided into two lobes, and the inner of these becomes secondarily divided into two." There are apparently no traces of lobation in the mandibles of *Blatta*. The outer of the three lobes of each maxilla becomes the palp, while the inner two become the galea and lacinia of the adult.

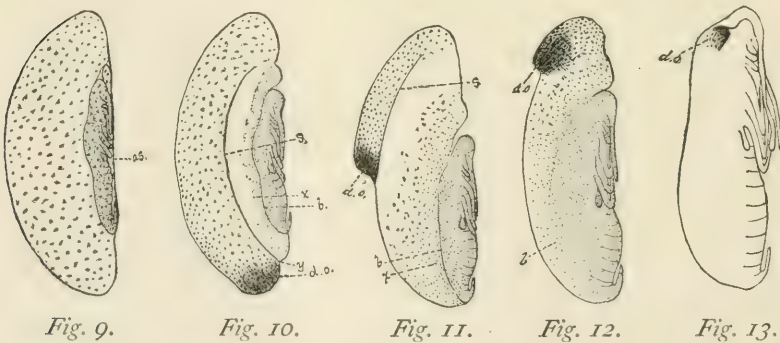


Figure 9.—Embryo of *Blatta*, 15 days old; revolution about to begin. The stages in revolution are represented, after the rupture of the amnion and serosa, in Figures 10-13, which are from embryos 16, 16½, 16¾, and 17 days old respectively. *as.* amnion and serosa; *s.* edge of serosa; *b.* dorsad growing body wall; *d.o.* dorsal organ; *x.* clear zone covered with scattered amniotic nuclei.

In *Blatta* the formation of the nervous system in its earlier stages cannot be clearly seen from the exterior. The same holds true of the small tracheal invaginations, though several pairs, especially those of the thorax and basal abdominal rings, may be seen on the pleuræ in good preparations before revolution. Still they are so much less distinct than in *Doryphora* that I have given them little attention.

The peculiar phenomena of revolution are hurried through by the embryo from the beginning of the sixteenth to the end of the seventeenth day. Several successive stages in the process are represented in the woodcuts (Figs. 9 to 13). When fifteen days old (Fig. 9) the embryo still occupies the middle of the ventral surface of the egg, the distance from the head to the cephalic end of the yolk being almost equal to the distance of the tail from the caudal end of the yolk. The amnion and serosa (*as*) still envelop the embryo, though they have become much attenuated. By the end of the fifteenth or the beginning of the sixteenth day, the envelopes rupture, an irregular slit being formed down the median ventral line. The amnion now appears to undergo degeneration, at least in part, while the serosa is drawn back from both sides by a contraction of the protoplasm of its cells, the large nuclei of which make it easy to trace all the steps in the formation of the dorsal organ.

Soon after the rupture of the envelopes the embryo and egg, when seen from the side, resemble Fig. 10. The embryo stands out free from its envelopes on the yolk; the edges of its dorsal growing walls (*b*) are distinctly marked. Near these, on the surface of the egg, are seen a number of scattered nuclei, which are of the same size as the nuclei of the cells forming the embryo. These I take to belong to the portion of the amnion which has become folded back on the yolk and forms a zone (*x*) extending the whole length of the yolk in contact with the dorsal growing body wall. Next to this zone lies another zone, which is bounded by the distinct edge of the serosa (*s*), and which I regard as a portion of the yolk left bare, as no nuclei are to be found on its surface. Besides the ventrodorsal contraction in the substance of its anterior edge (*s*), the serosa contracts in an antero-posterior direction, thus producing the constriction seen at *y* in Fig. 10. The rounded and projecting lump formed at the caudal pole is the beginning of the dorsal organ (Fig. 10 *d. o*). The



contraction continues towards the median dorsal line and towards the cephalic pole. In Fig. 11 the dorsal organ has moved half-way up the dorsal surface. Its darker color in stained embryos is due to the fact that the serosal cells have become deeply columnar with a consequent approximation of their large nuclei to one another. The embryo, besides increasing in size, has undergone a change in position. Its tail now lies at the caudal end of the egg. Notwithstanding the embryo's growth in length, its head lies much lower than in the preceding stage (Fig. 10). The body wall (*b*) is still distinct, the zone of sporadic amniotic (?) nuclei (*x*) has increased in breadth. As in the preceding stages, these nuclei are most closely aggregated near the edge of the advancing body wall. In the next stage (Fig. 12) the dorsal organ has reached the cephalic end of the yolk and bulges out like a large hood. The body walls of the embryo have nearly enveloped the yolk at the caudal end.

The next change takes place very rapidly. The stage represented in Fig. 12 is attained towards the end of the sixteenth day. By the seventeenth day the walls have closed in the median dorsal line, and the embryo has grown in length to such an extent as to bring its head to the cephalic pole. The dorsal organ has been shut in by, and lies immediately below, that portion of the body wall, which will form the tergum of the prothorax. On entering the yolk the cells of the dorsal organ begin to disintegrate. Two of the stages in the formation and dissolution of the dorsal organ are represented in Figs. 50 and 51, both from longitudinal sections, the former being sagittal, the latter frontal.

Figure 50 represents a section through the centre of the thickened mass of serosal cells. The deeply stained nuclei are seen crowded together in the inner ends of the cells, the contours of which are rendered papillose apparently by the pressure of the nuclei against the cell walls. The outer ends of the elongated columnar cells form a thick layer of granular protoplasm considerably depressed at *o*. This depression is equivalent to the tubular cavity in the dorsal organ of *Hydrophilus*.

In Fig. 51 the large lump of cells has become engulfed in the yolk. The body wall has closed over it, and the heart (*cc*) has formed between it and the ectoderm. The large deeply staining nuclei (*m*) are seen in the various stages of active degeneration,

many of which recall the degenerating nuclei in the entoderm of *Doryphora*. We have the same vacuolization of the karyoplasm and agglomeration of the chromatin. In the centre of the mass a pale, oval spot surrounds an elongated cavity (*o*), which is almost obliterated. This cavity results from the depression *o* of Fig. 50 by a closing in over it of the peripheral edges of the dorsal organ.

Figure 48, drawn from an advanced embryo saturated with clove oil, shows the condition of the different organs shortly before hatching. The embryo preserves the shape of the egg, being much flattened laterally. The segments of the body are all distinctly defined. The mouth parts have become closely approximated, and have assumed their definite relations to one another. The long antennæ (*at*) extend as far as the two anal stylets (*ast*) in which the ventrally bent tip of the abdomen terminates. The different divisions of the alimentary canal, œsophagus (*oe*), ingluvies (*c*), proventriculus (*gs*), stomach (*st*), still containing the remains of the yolk with its degenerating nuclei, and rectum (*rct*), ending in the anus posteriorly, and surrounded by a wreath of Malpighian vessels (*mpg*) anteriorly, may be readily traced in the figure. The heart is seen as a delicate tube just beneath the dorsal integument. The large supræœsophageal ganglion (*cgl*) connected with the large lateral compound eyes, in which the pigment is being deposited, fills the greater portion of the brain-box. One of the commissures is seen connecting it with the infraœsophageal ganglion (*gl*<sup>2</sup>). The three thoracic ganglia (*gl*<sup>3</sup>, *gl*<sup>4</sup>, *gl*<sup>5</sup>) are much larger than the six abdominal ganglia. A large, granular, fat body (*ad*) is applied to the inner surface of pleural wall of the abdomen. The refractive granules imbedded in it form a chevron in each of the first five or six somites. Patten (38) in his preliminary note on *Blatta* thus describes the physical and chemical nature of these bodies: "In the embryos of *Blatta*, as well as in those of most if not all other insects, there appears in each of the segments at a certain time a great number of clear, highly refractive particles that at first might be taken for oil globules, and which have always been regarded as such. On more careful examination, however, it will readily be seen that this supposition is incorrect. A number of tests have been made in order to ascertain the nature of these bodies, and the results show

that there are some salts of uric acid. That they are not of a fatty nature is indicated by the fact that treatment of the embryos with hot benzole, chloroform, or clove oil has not the slightest effect upon the bodies in question. Further examination with a high magnifying power shows that they consist of small spheres of an extremely refractive substance, from the centre of which dark lines radiate in an irregular manner, producing the same appearance seen in the crystals of urea from the Malpighian vessels. It was this similarity which first suggested the true nature of these bodies; and further tests confirmed this view, for, after heating an embryo with nitric acid upon a glass slide, and then adding a little ammonia, the characteristic red color of Murexid was formed. A still further test was formed by dissolving the granules in dilute caustic potash, and then precipitating the urea by adding acetic acid, although this method did not give such definite results as the first."

The embryonic development of *Blatta* is completed by about the thirtieth day from oviposition.

Figure 49 shows the embryo soon after hatching. Shortly after leaving its narrow place in the capsule, the insect undergoes a peculiar change in shape. While confined by the chorion the diameter from one pleural wall to the other is about one-third the dorsoventral diameter of the insect. Soon after hatching, its dorsoventral diameter is only about one-third as great as its greatest breadth. The tip of the abdomen, ventrally flexed in the egg, bends dorsally as indicated by the position of the anal stylets, which now point directly upwards and outwards. The spines and onychia, most abundant on the legs, are developed shortly before hatching.

### *Doryphora.*

*Doryphora* embryos, when carefully prepared, reveal much more in surface views than *Blatta* embryos prepared according to the same methods.

The last stage described is represented by Fig. 73. I shall pass over a few of the succeeding stages, and stop to describe the embryo represented in Fig. 72, which shows, with great clearness, all that has taken place in the omitted stages, and makes a description of them unnecessary. The figure is slightly

diagrammatic, being drawn from a number of different embryos, each of which contributed some of the details in a clearer and more pronounced manner. The mouth (*o*) and anus (*a*), both triangular depressions, have become clearly established. The former has in front of it a heart-shaped prominence, the bilobed labrum. The lateral half of the head presents some interesting facts, first elucidated in Patten's paper on the eyes of *Acilius* (39). Each half of the head is divided by longitudinal constrictions into three parallel rounded ridges, each of which is further divided by two transverse depressions into three subquadrangular thickenings. The three inner (*b*<sup>1</sup>, *b*<sup>2</sup>, *b*<sup>3</sup>) on each side, representing the three segments of the brain, are directly continuous with the ventral ganglion chain, extending to the protodæum. The row of prominences (*og*<sup>1</sup>, *og*<sup>2</sup>, *og*<sup>3</sup>) on the outer side of the three brain segments are the optic ganglion, the further three (*op*<sup>1</sup>, *op*<sup>2</sup>, *op*<sup>3</sup>), somewhat indistinctly seen because situated on the very edge of the head, are the divisions of the optic plate, each of which, in *Acilius*, according to Patten, bears a pair of ocelli. The only appendages of the head proper in this stage are the antennæ (*at*), which are directed backwards, and the heart-shaped labrum. The head also presents three pairs of small invaginations somewhat less distinct than in the figure (*t*<sup>1</sup>, *t*<sup>2</sup>, *t*<sup>3</sup>). These lie near the longitudinal constriction, separating the brain thickenings from the thickenings of the optic ganglion. This is best seen in the third segment, where the invaginations lie at the bases of the antennæ. Following the third segment of the brain is distinctly seen in some embryos a short segment inserted between the antennary and mandibular segments. Its short ganglionic swellings (*gl*<sup>4</sup>) are far apart, and connected by a broad commissure. This somite may also have a pair of small invaginations, but I have been unable to find them. Hereupon follow the mandibular, and the first and second maxillary segments, each with a pair of invaginations. Those of the second maxillary segment are concealed behind the bases of the elongated appendages, but are readily seen in sections.

The three broad thoracic segments are provided with the three pairs of legs, all of which are of the same length. The division into femur, tibia, and tarsus is indistinctly marked. In none of the preceding stages have I observed what is so prom-



inent in *Blatta*, viz. the appearance of appendages on the abdominal somites. There are not the slightest traces of even the pair of appendages of the first abdominal somite, which in *Blatta* develop into the large glandular organ of which I have treated elsewhere (50). The tracheal invaginations are situated at the bases of the legs. Those of the first thoracic segment are small, and soon close over and disappear. The second pair, which are almond-shaped, are the largest in the whole embryo, and so remain. They are situated near the constriction dividing the first from the second thoracic segment, and in later stages often have the appearance of belonging to the first segment. The metathoracic invaginations are somewhat smaller, and are also placed near the edges of the somite to which they belong. In the succeeding abdominal segments there is a tracheal invagination in the middle of each lateral half. These invaginations become successively smaller till they can be detected only with great difficulty on the 10th and 11th somites (*t* 19, *t* 20). The 11th somite is followed by the broad subhexagonal caudal plate with its large protodæal invagination. The corners of the plate are formed by rounded lobes containing apparently spherical bodies, the ends of the three pairs of Malpighian vessels. These grow off from the protodæum at an unusually early period in *Doryphora*, and turn back till their rounded blind ends terminate just beneath the surface ectoderm. The paired ganglionic thickenings are seen in the embryo figured to be slightly kidney-shaped with their hili directed laterally. The *Mittelstrang* is apparent in the small and nodular intersegmental thickenings (*mst*), which appear from the surface as small masses of cells of a somewhat different nature from those of other portions of the median line.

The surface changes which the embryo undergoes in the stages immediately following that represented in Fig. 72 may be briefly summarized. The embryo just described lies like a band on the ventral yolk, the caudal portion still extending round the hind pole of the egg, and up the dorsal surface a short distance. The isochronous changes which ensue are, (1) a shortening of the embryo, bringing the tail to the pole of the egg; (2) a broadening of the embryo, the sides of which now bend dorsally and clasp the yolk; (3) a greater concentration of the cephalic, mandibular, and maxillary somites to form the

head of the larva, and (4) an increase in the length of all the appendages except the antennæ. The shortening of the embryo stops as soon as its tail reaches the caudal pole of the egg, the lateral growth of the body continues, and we reach the stage figured (Fig. 74). The yolk is not yet covered by the dorsad growing walls of the embryo. The head is distinctly marked off from the thorax, the wide-spread mouth parts of Fig. 72 have converged, and are assuming the relations which they bear to one another in the larva. The ventral nerve chord has developed considerably, and it is now possible to recognize near the centre of each ganglion the mass of "Punksubstanz" definitely marked off from the cellular portion and united with the corresponding mass of its fellow-ganglion by two-cross commissures.

Figure 75 represents the larva ready to hatch. The dorsal body wall has closed, the six ocelli have become pigmented, the cuticle has developed spines, the meso- and metathoracic and first abdominal segments have each developed a short, sharp, black spine in a line with the abdominal spiracles. These spines are used by the larva in rupturing the chorion, the vitelline membrane, and the various cuticles which it has shed before reaching this stage. The movements of the hatching insect at first produce a rent in the chorion extending from the first to the third spine, by further struggling the two rents from opposite sides are made to meet over the head, and the insect emerges from between the two lips thus formed. The embryonic development requires about six days.

Before passing on to a description of the internal changes of *Doryphora* and *Blatta*, it is necessary to consider the fate of the embryonic membranes of the former insect. This is very different from what was observed in *Blatta*. The serosa, instead of rupturing when the amnion ruptures, separates from it and also from the entire surface of the yolk, and forms a third egg envelope, beneath the vitelline membrane, to which it applies itself. It remains clearly recognizable by its large and deeply staining nuclei till the insect is almost ready to hatch (Fig. 86 *sr*), when it disappears, probably by absorption. The fate of the amnion is peculiar. On rupturing, its two ventrally bent folds turn back and become in part applied to the yolk. A few of its cells are loosened from the bulk of the membrane, and are often seen sticking to the serosa at different points. They are probably

endowed with amœboid tendencies, for when the ectodermic wall is about to be completed in the median dorsal line these cells are seen to have accumulated at the place of closure. The amniotic cells, which have become applied to the surface of the yolk by the bending back of the two folds resulting from rupture, have closed in the yolk while the serosa is separating from it. The advancing body walls of the embryo, however, soon make the amniotic covering unnecessary, and it contracts in the median dorsal line to form what may be called an *amniotic* dorsal organ, to distinguish it from the *serosal* dorsal organ of *Blatta*. Figure 90 is a part of a section through the median dorsal portion of an embryo in the stage represented in Fig. 74. At *do* the protoplasm of the amnion has thickened, and the nuclei are seen passing in between the yolk bodies. At *m* are a number of nuclei undergoing degeneration. These resemble the degenerating entoderm nuclei to which I have called attention in a much younger stage. The amnion cells, which have become applied to the yolk when the membrane ruptures, enter the yolk after the formation of the dorsal organ by the very narrow slit left in the closing ectoderm in the median dorsal line. This is seen somewhat indistinctly in Fig. 85. Nuclei are observed at *b* passing in between the two cardioblasts (*cb, cb*), which are about to meet and form the heart. The splanchnic mesoderm (*slm*), with the underlying entoderm, still leaves a wide gap through which the migration into the yolk takes place. The granular matter surrounding the nuclei is probably the remains of the cytoplasm of the amnion cells. In the figure a number of entire

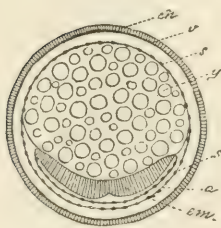


Fig. 14.

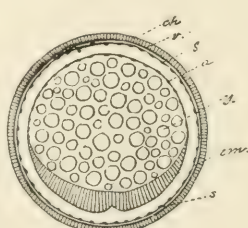


Fig. 15.

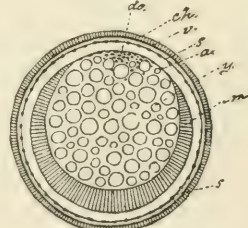


Fig. 16.

Figures 14-16. — Three diagrammatic median cross-sections through the egg of *Doryphora*, before and during revolution. *ch*, chorion; *v*, vitelline membrane, applied to the inner face of the chorion; *a*, amnion; *s*, serosa; *em*, embryo; *do*, dorsal organ (amniotic); *y*, yolk.

amnion cells (*a*) are still seen just beneath the serosa, and one is seen right at the narrow space between the cardioblasts. The last steps in the process are represented in Fig. 93. The dorsal ectoderm has become continuous at *ect* in the median line. The two cardioblasts are still in the same stage. One of the last amnion nuclei is passing in surrounded by a mass of granules. A clear idea of the revolution of the embryo *Doryphora* may be obtained from the three stages in the diagrams.

The method of revolution just described is very similar to that observed by Graber (15) in *Lina*. Though he did not give a description of the complete process, he made the important observation that *the serosa remains unchanged till after the chitinous cuticle is formed*.

#### GENERAL REMARKS.

##### *Dorsal Organ.*

The term "dorsal organ" has been applied to the peculiar thick lump of cells resulting from the concentration on the dorsal yolk of the remains of either the amnion or serosa, or of both, preparatory to their sinking into the yolk and being absorbed.

A similarity in form and position has led many investigators to look for an homology between the dorsal organ of insects and the homonymous organ of the Crustacea.

My observations on the dorsal organ of *Cymothoa* have convinced me that there are fundamental differences between the Crustacean and Hexapod dorsal organ. First, the dorsal organ of this form, and probably other Isopoda, is a structure which persists from an early stage almost to hatching, and may persist throughout life in some Branchiopoda, whereas the dorsal organ of insects is a very transitory structure. Secondly, the dorsal organ of *Cymothoa* seems to be a secretory organ, as was deemed probable by Balfour (2). I have observed that the elongated cells which form the organ secrete a reniform sack of chitin, which is joined by means of a corrugated chitinous tube to the cuticle shed from the surface of the embryo at a very early stage. Nusbaum (34) has observed that the cavities of the dorsal organs of *Mysis* are filled with a clear substance, probably a secretion.

The presence of the so-called dorsal organ in insects is prob-



ably due to the fact that the embryonic envelopes are to be absorbed. As these membranes consist of assimilable matter, it is obviously an advantage to the embryo to be able to add them to the stock of food represented by the yolk. The simplest conceivable method of effecting the resolution of the envelopes into food material, considering their position when fully developed, would, of course, be to engulf them in the yolk, where, under the influence of the yolk cells, metabolism is being actively carried on. There are two methods of inclosing the membranes in the yolk. According to one, they might undergo dissolution *in situ*; according to the other, they might be brought together in a mass and swallowed up by the yolk somewhere in the median dorsal line. Obviously the latter method is the more advantageous, as the body walls, continually growing towards the median dorsal line, might be impeded in their advance if the membranes were absorbed at all points on the surface of the yolk. Probably the inconvenience which would thus result from a diffuse absorption accounts for the fact that it does not occur, though a modification of the method occurs in *Doryphora*, where the serosa is absorbed very late in development after the larva has secreted its second cuticle and is almost ready to leave the egg.

Given a thickening, somewhat flattened mass of cells, destined to be swallowed up in the yolk, and it is most natural to suppose that the organ, in passing into the yolk, would become cup-shaped as in *Blatta*, or form a thick-walled tube, if the organ extended the full length of the dorsum, as in *Hydrophilus*. In either case the outer ends would be made to converge, by the lateral pressure of the yolk and the sinking of the median portion of the organ, and we should get a closed tube or sack. This would not, of course, hold true of an organ formed like the amniotic dorsal organ of *Doryphora*, for the reason that in this case the decomposition begins as soon as the organ is formed, and not after it has passed into the yolk, as is the case with the serosal dorsal organs of other forms (*Hydrophilus*, *Blatta*, *Neophalax*). Hence the cavity of the Hexapod dorsal organ would resemble the cavity or so-called micropyle of the Isopod dorsal organ, though the two cavities would not be homologous.

## THE FATE OF THE DIFFERENT GERM LAYERS.

A. *Entoderm.*

Recent writers on insect embryology have recognized two forms of entoderm, — one called primary, and represented by the yolk cells; and one secondary, represented by the epithelial wall of the mesenteron. In *Blatta* the yolk nuclei steadily increase in size from their first appearance at a time when they are no larger than other nuclei. At the time of the formation of the dorsal organ they are by far the largest nuclei in the egg (Fig. 51 *v*). Their chromatin is distributed through the karyoplasm in the form of a fine, convoluted thread, and as two or more nucleoli (Fig. 54 *v*). Soon after the closing-in of the yolk, they lose their rounded outline, and become irregular and more homogeneous (Fig. 55 *v*). In the last stages of their dissolution they may be seen as stellate spots in the remains of the yolk aggregated in the stomach of the advanced embryo (Fig. 48). Yolk segmentation, though occurring in *Blatta*, takes place after the appendages are formed, at a much later period than in *Doryphora*. The segments, usually very obscurely defined, become confluent again as development continues.

In *Doryphora* the yoke cells undergo no increase in size from the time of their first appearance; but soon after the yolk has become segmented their cytoplasm is reduced to a scarcely perceptible layer surrounding the nucleus, which has become irregularly polygonal (Fig. 83). As all the eggs I studied were killed and preserved in the same manner, this difference in form between the yolk nuclei in the stages during yolk segmentation and after this process till the setting-in of degeneration, must be regarded either as a normal change in the living nuclei, or as indicating that their chemical nature is changed, and their resistance to the altering effects of reagents lessened.

After the completion of the mesenteron at a time when the larva is almost ready to hatch, the remains of the yolk nuclei are pushed back into the stomach in the same way as in *Blatta*. Here they degenerate in a manner very similar to that observed in the secondary entoderm nuclei, and the nuclei of the amniotic dorsal organ. They become swollen and vesicular, and their chromatin is reduced to irregular masses. The yolk becomes a compact, granular mass, staining pink in borax carmine.

The origin of the secondary entoderm in *Doryphora* has been treated of at length in preceding paragraphs. We have now to trace its fate, from the condition in which we left it, as two masses, — one under the blind end of the œsophagus, and the other under the blind end of the proctodæum. In an embryo of the stage of Fig. 72, each of the isolated masses has begun to send out the two bands of entoderm. These diverge from their point of origin, and apply themselves to what is to be the splanchnic mesoderm (Fig. 78 *ent*). Their divarication is so slight that a thick longitudinal section will sometimes include a whole band, if still short. Thus, in Fig. 92, from a section through an embryo in the stage of Fig. 72; passed to one side of the median line, we have the entoderm (*ent*) still attached to the mesoderm (*msd*), which is now distinctly marked off from the ectoderm of the stomodæal invagination (*st*). The entoderm is attached to the inner end of the œsophagus, and extends along the yolk as a band two or three cells thick. It is clearly distinguishable from the mesoderm by the greater clearness of its cells, and by its paler nuclei. The process at the posterior end of the embryo is similar, as may be concluded from Fig. 76, from the same embryo. Like the anterior thickening, the posterior mass does not remain stationary, but grows out in two bands. Thus it happens that little entoderm is found right under the proctodæum. The knife has not passed through the proctodæal invagination in the figure, but has cut to one side of the median line, through the Malpighian vessels *mpg*<sup>1</sup> and *mpg*<sup>2</sup> of Fig. 72. The true relations of these vessels may be understood from an examination of Fig. 77, and the present section, Fig. 76. The strand of entoderm, very similar to the anterior strand described above, is attached to the proctodæal pocket near the point at which one of the first pair of Malpighian tubes (*mpg*<sup>1</sup>) turns out toward the surface of the embryo, pushing aside the mesoderm, which elsewhere forms a continuous sheet under the ectoderm.

In the same figure may be noticed a second mass of entoderm (*ent*) attached to the proctodæum near the point at which the third pair of Malpighian tubes branches off from the common proctodæal pocket. This mass ends with a sharp point between two yolk segments. I have seen similar masses of entoderm in a few other embryos, apparently independent of the two main

forward-growing strands, and terminating in the same acute point which seems to force its way between the yolk segments. These points of entoderm do not grow far, as I have concluded from an examination of slightly older stages, but soon fuse with the bases of the two main strands, and form a meniscoid mass in every way comparable with the watch-glass-shaped mass in *Musca*, as described by Kowalevsky (27).

A median cross-section of an embryo, with the entoderm bands fully established, but not confluent, is shown in Fig. 78. The embryo is cut in two places. The upper half passes through one of the basal abdominal segments, while the lower half passes through the abdomen, a short distance from the tail. In the upper half no entoderm cells are to be found, as the two bands have not yet reached in their forward growth the basal abdominal segments in which they fuse with the two bands growing back from the stomodæal invagination. In the lower half a heap of succulent entoderm cells is seen on each side, separated from the coelomic cavity (*cl*) by the splanchnic mesoderm (*slm*).

Four stages in the formation of the mesenteron after the establishment of the entoderm as two long bands, are represented in Figs. 83 to 86 *ent*. The entoderm remains throughout embryonic development perfectly distinct from the splanchnic mesoderm, to which it is nevertheless very closely applied. At first the cells are irregularly arranged in the band which is deepest in the middle, but gradually flattens out to a single cell in thickness at its dorsal and ventral edges (Fig. 83). In a later stage, however, the nuclei have their long axes directed at right angles to the long axes of the splanchnic mesoderm cells (Fig. 84), and thus indicate that the cells of the entoderm are beginning to assume a definite columnar arrangement, though they still lie, in some places, in two or more rows, one above the other. By the time the body walls are about to close, the cells of the entoderm have formed an even layer of columnar elements (Fig. 85), an arrangement which is retained in all the subsequent stages till the embryo hatches.

The growth of the entoderm, accompanying the adjacent mesoderm and ectoderm in their dorsad movement, is at first largely along the dorsal edges of the bands, as may be seen by comparing Figs. 84 and 85, where the distance between the ventral edges of the two bands is nearly the same, while the



distance between the dorsal edges is greatly lessened. The transformation of the original ribbon of several superimposed rows of cells into the simple epithelium of columnar cells is not entirely due to cell division. As may be seen from Figs. 84 and 85, either the wandering of the inner rows of cells over the outer towards the dorsal edge of the ribbon, or a stretching of the whole band, so as to permit an intercalation of the cells of the inner rows between those of the outer row, are the more probable factors in the thinning out of the entoderm. The latter method is more probable, though the former method is certainly in keeping with the gliding and mobile movements of the entoderm. The nuclei of the entoderm have their chromatin distributed in the typical filament, which is more attenuated than in either mesoderm or ectoderm nuclei. Shortly before hatching the chromatin of the mesenteron nuclei appears to have dissolved, as they seem to have become perfectly homogeneous, though they still stain deeply. In the hatching larva the cells have become more deeply columnar, on account of a diminution in calibre of the mesenteron. The nuclei cease to absorb more of the staining fluid from the surrounding cytoplasm, though the walls retain their evenly rounded contour. Such a fundamental change in the nuclei would seem to indicate that some important change is about to take place in the mesenteric layer of cells; but whether this change is dissolution I am unable to say, as I have not studied the insect in the stages beyond hatching.

The process of mesenteron formation is essentially the same in *Blatta* as that just described for *Doryphora*. From the first, the entoderm cells of *Blatta* are as small and indistinct as the yolk cells are large and prominent. They form, as stated above, two bands of very flat cells bearing the same relations to the mesoderm as the corresponding bands of *Doryphora* (Fig. 54 *ent*). The edges of the two ribbons continue their growth, and meet ventrally and dorsally, to complete the mesenteron (Fig. 55 *ent*).

Besides the lining of the mesenteron the *corpus adiposum*, represented during the embryonic life of *Doryphora* by a number of granular cells which constantly increase in size up to the time of hatching, probably originates from the entoderm. I have observed in several cases that before the two posterior bands of

entoderm have reached the middle of the embryo a number of granular and somewhat larger cells are to be found mingled with the cells of the bands. I conclude that these cells are of entodermic origin because when first seen they are associated with the entoderm cells and resemble them more closely than they resemble the adjacent mesodermic elements. At first small (Fig. 85 *ad*), these fat cells gradually but constantly increase in size, their cytoplasm and nuclei increasing in about the same ratio. They wander about in the body cavity, but finally attach themselves to the ectodermic body walls, especially in the posterior two-thirds of the embryo on each side of the heart (Fig. 86 *ad*). They remain more or less globular or oval, the side in contact with the wall hollowing out a concavity in the cells of the ectoderm. The granulation of the cytoplasm which first distinguishes the fat cells from the true entodermic elements becomes coarser with the increase in volume. In the embryo ready to hatch the adipose cells have acquired gigantic dimensions, being many times the size of those represented in Fig. 86. Both nuclei and cytoplasm stain deeply, so that these fat cells are rendered among the most conspicuous objects in a section.

#### B. *Mesoderm.*

In *Doryphora* as soon as the gastrular tube has collapsed, the polygonal mesodermic elements form a layer several cells in thickness, applied to the inner surface of the median ventral ectoderm (Fig. 65 *msd*). This layer of cells thins out at its lateral edges. With the first traces of segmentation in the outer layer the mesodermic layer also divides, though incompletely, at the same places of constriction (Fig. 82). Soon the single intersegmentally divided band of mesoderm splits in the median line so that each segment contains two subquadrangular flattened masses. The coelomic cavity is formed at the outer edge of each of the masses by a separation of the cells of the two layers (Fig. 78 *cl*). The inner constitutes the splanchnic mesoderm, while all the remainder of the mesoderm constitutes the somatic layer (Fig. 78 *slm*). When the appendages appear, it is the latter layer of cells which supplies their cavities with muscle-forming cells; the portions inclosing the coelomic cavity accompany the adjacent ectoderm in its dorsad growth. As

soon as the growth in this direction is fairly started the ectoderm bulges out (Fig. 83 *ect*) and, drawing with it the somatic mesoderm, leaves a cavity between the yolk and the embryo which soon communicates with the coelomic cavity and assumes large dimensions (Fig. 84). Through the body cavity thus formed a thin plasma found as coagulated masses in hardened embryos probably circulates.

The cell *cb* (Fig. 83), which is recognized even at a much earlier stage by its peculiar form, and which is destined to take part in the formation of the heart, is the only element still uniting the splanchnic and somatic layers. This cell, as may be clearly seen in Figs. 83 and 84 *cb*, is triangular in cross-section, and inserts one of its acute angles between the yolk and the ectoderm. As this cell with those of exactly the same shape anterior and posterior to it form the heart, I shall call it a cardioblast. The true shape of the cardioblasts may be seen in a thick frontal section (Fig. 89) through the embryo of which Fig. 84 is a cross-section. Here the compact row of crowded but regular heart-forming elements (*cb*) is seen running between the actively proliferating entoderm cells (*ent*) on the one hand, and the mesoderm cells (*msd*) on the other. These last are somewhat scattered in the space between the cardioblasts and the thickened ectoderm.

In the more advanced embryo (Fig. 85) the cardioblasts (*cb*) from either side are near together. They have retained their characteristic form and position, while the somatic mesoderm has been converted into muscles (*msl*) and connective tissue, and the splanchnic layer (*slm*) has applied itself closely to and is coextensive with the single-celled layer of entoderm (*ent*). In Fig. 86 the heart is completed. A glance at this figure and Fig. 85 shows the manner in which the two cells from opposite sides unite. Though forming the two halves of the tube in Fig. 86, they still show the three angles which were apparent just after the formation of the coelomic cavity. The heart remains in the condition shown in Fig. 86 till the embryo hatches. I have not studied the formation of the blood in *Doryphora*.

My observation on the formation of the sexual organs, though more complete than in *Blatta*, are still very fragmentary. These organs originate as two elongate thickenings of splanchnic

mesoderm, one on each side projecting into the body cavity. Later (Fig. 84 *gn*) they become rounded and are attached by a thin band of splanchnic mesoderm only. I have seen the much attenuated duct leading from each organ to the exterior, but have made no observations on its origin. The ducts converge posteriorly, but end by separate openings on the 11th abdominal somite; thus presenting a condition which in Ephemerids is permanent throughout life, according to Palmén (37). There is probably some connection between the two pairs of very indistinct tracheal openings in the 10th and 11th somites and the openings of the efferent ducts, but I was unable to determine whether the large sexual openings originate by enlargement from a single pair of these tracheal openings, or from the confluence of all four to form two orifices. The cross-section (Fig. 80) includes the openings of the efferent ducts (*go go*), the knife having taken away a very thin layer of surface cells.

Up to the formation of the coelomic cavities the mesoderm of *Blatta* closely resembles the same layer in *Doryphora*. With the evagination of the appendages from the entoderm a decided difference is, however, observable. Each coelomic segment, if situated in an appendage-bearing segment, instead of retreating dorsally as in *Doryphora*, sends a diverticulum into the appendage. This is clearly seen in Fig. 53 *cl*, a cross-section from an embryo twelve days old. The cells of the diverticulum develop into the muscles of the appendage, and together with a portion of the mesodermic layer still remaining in the body cavity are shut off from what probably represents the true coelomic cavity (Fig. 54 *cl*). The further changes again resemble those in *Doryphora*. Long before the heart is formed and the lateral walls have met in the median line, the body walls of the embryo are observed to pulsate regularly like the body walls of *Gryllotalpa*, as described by Korotneff (25). As in *Doryphora* a plasma is at this time found in the body cavity which is divided by films of connective tissue into a great number of small intercommunicating lacunæ (Fig. 54). In regard to the primitive blood sinus, my observations confirm Patten's (38). He says: "The primitive blood sinus is the space between the somatic and splanchnic mesoderm, divided into a number of smaller and irregular sinuses by meshes of connective tissue, some cells of which, in the earlier stages, become free and form the blood capsules. By



the pulsation of the mesodermic folds, long before a special heart is formed, a circulation through the body cavity is brought about like the circulation in many of the lower worms."

One of the stages in the formation of the heart is seen in Fig. 52. The cardioblasts (*cb cb*) are both more numerous and more irregular than in *Doryphora*. They unite to form a tube, the lumen of which is at first oblong in cross-section (Fig. 52 *h*). In the cardiac walls amœboid cells are occasionally seen (*bl*), which loosen themselves from the mesodermic elements and pass into the lumen of the tube, probably to form blood corpuscles.

### C. Ectoderm.

My observations on the organs derived from the ectoderm are limited almost exclusively to *Doryphora*.

The hypodermis of the embryo secretes two cuticles, the second of which covers the larva, while the first is cast off at the time of hatching. Shortly before hatching the embryo is confined by four loose envelopes,—the chorion, the vitelline membrane, the serosa, and the first cuticle. Graber (15) has made a similar observation on the embryo *Lina*.

The three broad-based chitinous spines used by the insect in rupturing its envelopes, and which are analogous to the frontal spine observed in *Strongylosoma* by Metschnikow (31) and the deciduous claw on the beaks of birds, are secreted by pyramidal thickenings of the hypodermis (Fig. 86 *hsp*), the cells of which are much lengthened, though forming a single layer.

In the surface views of the embryo (Fig. 72) it is possible to trace the origin of all the ganglia as paired thickenings of the outer layer. At first these thickenings differ histologically in no particular from the surrounding ectoderm (Fig. 78 *nr*). Gradually, however, the cells in the centre of each thickening enlarge, while their cytoplasm becomes drawn out into fine threads. At the same time all the ganglion cells thus formed arrange themselves in such a way as to have their threads intermingle. *This mass of intertwined threads becomes the Punktsubstanz* (Fig. 94 to 104 *pct*). The outer layer of cells (*e*) continuous with the hypodermis (*ecd*) stands off somewhat from the ganglionic thickenings, leaving a space which is in early stages occupied by several large, clear, oval cells (*gbl*), which divide

rapidly by karyokinesis, and might be called *ganglioblasts*, as the products of their divisions reinforce the mass of ganglion cells. In a series of sections through the mesothoracic pair of ganglia (Figs. 94 to 104) the Mittlestrang may be readily traced. The shape of its cross-section varies with the plane of section through the ganglion and its cross or longitudinal commissures. At the two points in the ganglion where the two pairs of Punktsubstanz masses fuse to form the commissures *c cm*, the Mittlestrang is in great part obliterated. The median strand is largest where the two longitudinal commissures are passing into the anterior ends of the three thoracic ganglia. *Here they persist in the larva, while completely disappearing elsewhere, and become converted into the three chitinous furcæ, each one of which is just in front of a thoracic ganglion.*

Figure 105, from a section through the fore end of the meta-thoracic ganglion, shows the Mittlestrang portion (*mst*) continuous with the hypodermis (*ect*) and broadening out into the furca (*f*) after passing between the two halves of the ganglion (*gl*). Muscles (*msl*) are attached to the two divergent ends. The mesothoracic furca, which is formed in exactly the same manner, is seen in Fig. 86 *f*, where it passes between the commissures (*cm*); its connection with the muscles is seen at *r*.

A frontal section (Fig. 91) shows the structure of the meso- and meta-thoracic ganglia after they have become loosened from the surface ectoderm. The longitudinal (*cm*) and cross-commissures (*c cm*) are clearly seen as white Punktsubstanz separated from the ganglionic cells by the inner neurilemma (*inrl*). The outer neurilemma (*onrl*) is also developed, as are also the two main nerve trunks (*n*<sup>1</sup>, *n*<sup>2</sup>), the anterior of which bifurcates (*n*) while leaving the ganglion.

The separation of the nervous system from the integumentary ectoderm progresses from before backwards. The two brain masses separate first. The first segment becomes very small and possibly disappears. The three segments of the optic ganglion are invaginated and pushed under the optic plate in a manner which I believe to be similar to that described by Patten (39) in *Acilius*, though I have not followed the details of the process. *The frontal ganglion is formed as an unpaired thickening of the dorsal wall of the œsophageal ecto-*

derm near the base of the labrum. Punktsubstanz is formed in this ganglion in the same manner as in the brain and ventral ganglia. It is ultimately loosened from the stomodæum, and becomes surrounded by mesodermic elements. Later the four pairs of ganglia of the intercalary, mandibular, 1st and 2d maxillary segments fuse and form the infracæsophageal ganglion.

*That the outer neurilemma is of ectodermic and not of mesodermic origin seems to be proved by the fact that shortly after the separation of the nerve-chord from the integumentary ectoderm, it sheds from its surface a delicate chitinous cuticle simultaneously with the shedding of the first integumentary cuticle.* This cuticle, which is separated from the surface of the outer neurilemma, and even from the surfaces of the main neural trunks, is afterwards absorbed.

The six ocelli are formed as apple-shaped thickenings of the optic plate. Their small size has hindered me from studying their structure in detail. I have represented in Fig. 81, soon after their first appearance, two of the ocelli corresponding to the eyes of *Acilius* numbered V. and VI. by Patten. Each forms a slight depression somewhat paler than the surrounding ectoderm. The nucleus (*n*) of one of the central cells is seen to be much larger than the nuclei of the surrounding cells. Patten has described and figured this same large nucleus in the eyes of *Acilius* (Pl. XI., Figs. 63, 64, 65, etc.).

*The five pairs of invaginations anterior to those of the second maxillary segment form the tentorium of the larval head.* These invaginations grow inwards as slender tubes, which anastomose in some places. Their lumina are ultimately filled with chitin. Palmén (36) found that the tentorium of *Ephemerids* breaks across the middle during ecdysis, and that each half is drawn out of the head, like the chitinous lining of a tracheal tube. This fact, together with my observations on the tentorium of *Doryphora*, makes it highly probable that, as Palmén suggests, the tentorium is formed from tracheæ, which have become modified for muscular attachment.

Of the true tracheal invaginations, those of the pro- and meta-thorax disappear. The mesothoracic spiracle comes to lie between the pro- and meso-thoracic segments near the base of the legs and ventral to the line of abdominal spiracles. This first spiracle is the largest, and in cross-section appears as a

short, chitinous cylinder, projecting somewhat from the general surface of the segment. Its inner walls are lined with spines which are directed outward. The abdominal spiracles, though smaller, are also lined with similar spines (Fig. 85 *tr*). The first pair of tracheæ send large branches to the head. The abdominal tracheæ of each side of the body anastomose to form a longitudinal trunk, from which the branches ramify to the different organs. The invaginated ectoderm, at first very thick (Fig. 84 *tr*), gradually thins out as the respiratory tubes lengthen and ramify. The thin epithelium thus formed secretes the chitinous lining provided at the time of hatching with the spiral thickenings so characteristic of insect tracheæ.

The proctodæum and stomodæum when first formed are triangular in cross-section. Later both become hexagonal (Figs. 79 and 80). A like pronounced similarity in form between the stomodæum and proctodæum of *Gammarus* has been observed by Pereyaslawzewa (40). She says: "Fait très intéressant, qui mérite d'être noté, c'est qu'à mesure de l'acroissement du rectum et de l'œsophage, leur partie intérieure affecte absolument la même forme carrée, dont les parois sont concaves. Ce qui concerne la configuration des cavités, elles n'en diffèrent aucunement et se dessinent sous forme d'une croix oblique; la dissemblance consiste en ce que dans l'œsophage ce sont les parois qui s'enfoncent, tandis que les parois du rectum sont tapissés d'un epithelium cylindrique, dont les cellules s'aplatissent graduellement vers les angles."

The three pairs of Malpighian vessels appear at a very early period, while the proctodæal invagination is still very shallow. They are from the first hollow diverticula, and have their blind ends pushed back by the forward growth of the proctodæum. Thus it happens that a transverse section through the tail-end of an embryo in the stage of Fig. 74 passes through both the proctodæum and the Malpighian vessels (Fig. 79, *x*, *mpg*, *mpg*). When the blind ends of the six tubes have struck the body wall, their continued growth forces them to turn and grow forward. After the formation of the dorsal body wall, they may be found lying as thin undulating tubes, surrounding the mesenteron at approximately equal distances from one another (Fig. 86 *mpg*).

The very early appearance of the Malpighian vessels and their paired arrangement in *Doryphora*, Fig. 72, would seem to



indicate that at one time they opened on the surface of the body, and that their orifices were subsequently carried in by a deepening of the proctodæal invagination. Possibly these tubes in insects are homologous with the anal tubes of the *Echiurus* larva, which are modified segmental organs. Gegenbauer (14) has intimated the possible derivation of the Malpighian vessels from paired tubes opening on the outer surface of the body. He says: "As they [the Malpighian vessels] are formed at the same time as that portion of the hind-gut, which in the embryo is developed from the ectoderm, it is not improbable that they primitively opened on the surface of the body, or were derived from organs which did so. In all divisions there are two chief canals, as is often seen at the point where a large number of canals open and unite. This number may therefore be regarded as a primitive character."

MILWAUKEE, Sept. 12, 1888.

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## DESCRIPTION OF PLATE XV.

*Blatta germanica.*

FIG. 1. Piece of chorion from lateral face of oöthecal egg.

FIG. 2. Piece of chorion from micropylar area with micropyles. *a*, aperture of micropyle; *b*, tubule.

FIG. 3. Transverse section through the crista of a capsule. *o*, oöthecal wall splitting into two laminae, *o*<sup>1</sup> and *o*<sup>2</sup>; *cr*, crystals of calcium oxalate; *ep*, remains of follicular epithelium.

FIG. 4. Longitudinal section of epithelial cap on the germarium pole of the egg. *ep*, follicular epithelium; *ch*, chorion secreted by the same; *a*, the point at which the chorion widens, showing its lengthened trabeculae; *b*, pyriform dilatation of the chorion; *pr*, protoplasm of the Keinhaut, containing numerous bacteria-like corpuscles.

FIG. 5. A number of cells from the follicular epithelium. *a*, resting nucleus; *b* and *c*, nuclei in akinetic division.

FIG. 6. Longitudinal section of immature ovum 1 mm. long, being the circumnuclear portion in the centre of the dorsal concavity of the egg; nucleus amœboid just after reaching the surface. *n*, chromatin particles; *x*, layer of small yolk bodies just beneath the epithelium.

FIG. 7. Same section of an egg 2 mm. long. Nucleus emarginate on outer surface, giving off the maturation sphere *b*; *y*, small yolk bodies under the epithelium.

FIG. 8. Section at right angles to that in Fig. 7, of a nucleus in the same stage. *b*, cavity into which the maturation spheres fitted; *pn*, paranucleolus.

FIG. 9. Nucleus in the same stage; *pn*, paranucleolus. Egg 2 mm. long; section in the same plane as Fig. 7.

FIG. 10. Longitudinal section of median dorsal surface of an egg 2.5 mm. long. Particles of chromatin aggregating into a somewhat stellate central mass.

FIG. 11. Longitudinal section corresponding to Fig. 10 of an egg somewhat older, 2.8 mm. long. A delicate wall encloses the particles of chromatin.

FIG. 12. First polar spindle in the metakinetic stage. Egg mature.

FIG. 13. First polar spindle in anaphasis. Egg mature.

FIG. 14. Median longitudinal section through the dorsal surface of an oöthecal egg 4 to 6 hours old. *pgl*, first polar globule; *x*, second polar spindle in metakinesis.

FIG. 15. Longitudinal section through both polar globules, 3 to 4 hours older than egg represented in Fig. 14.

FIG. 16. Surface view of the median dorsal portion of an oöthecal egg about 10 hours old. *pgl pgl*, polar globules; ♀ *pn*, female pronucleus (out of focus).

FIG. 17. Median longitudinal section of dorsal portion of an oöthecal egg. *a*, dorsal contour; ♀ *pn*, female pronucleus just after leaving the polar globules.

FIG. 18. Longitudinal section of circumnuclear region, from near the middle of the homogeneous yolk, with female pronucleus. The arrow in this and the following figures points in the direction of the cephalo-caudal axis of the egg.

FIG. 19. Longitudinal section of circumnuclear portion of egg, one-third the length of the egg from the cephalic pole. *a*, dorsal contour; ♀ *pn*, female pronucleus; ♂ *pn*, male pronucleus.

FIG. 20. Longitudinal section of circumnuclear area from middle of homogeneous yolk. ♂ *pn* and ♀ *pn*, male and female pronuclei conjugating.

FIG. 21. Longitudinal section of circumnuclear area from the middle of the front portion of the homogeneous yolk. Cleavage nucleus.

FIG. 22. Cleavage nucleus preparing to divide. *cp*, cytoplasm.













## DESCRIPTION OF PLATE XVI.

*Blatta germanica.*

FIG. 23. Cleavage nucleus dividing. *a*, points to the ventral contour. The nucleus in this egg had moved out into the granular yolk some distance.

FIG. 24. Two nuclei; *a*, seen in lateral, and *b*, in polar view, from an egg containing 4 nuclei in the metakinetic stage of division.

FIG. 25. Ventral third of a transverse section of an oöthecal egg; *a* and *b*, cells which have just reached the surface. The amoeboid cell in the interior is on its way to the surface.

FIG. 26. Corresponding section of the somewhat older egg (Fig. 36). *a*, a group of cells formed by tangential akinesis from one of the nuclei, like *a*, Fig. 25.

FIG. 27. Ventral third of a transverse section of an egg in the blastoderm stage; 6 days old.

FIG. 28. Ventral third of a transverse section. Blastoderm contracting. At *x'*, yolk nucleus being given off; at *x*, one which has sunk deep into the yolk.

FIG. 29. Transverse section through *e*, of an embryo like the one represented in Fig. 43. *v*, yolk-cell; *msd*, mesoderm; *ecd*, ectoderm.

FIG. 30. Transverse section through *e'* of the embryo 43. *am*, amnion; *sr*, serosa; *ecd*, ectoderm; *msd*, mesoderm; *v*, yolk-cell.

FIG. 31. Transverse section through the point *pcl* of Fig. 41. *ecd*, ectoderm; *v*, yolk-cell; *msd*, mesoderm.

FIG. 32. Transverse section through a point a little in front of *as* of Fig. 43. *am*, amnion; *sr*, serosa; *ecd*, ectoderm; *msd*, mesoderm; *v*, yolk-cell.

FIG. 33. Surface view of blastoderm, showing the binucleolate nuclei.

FIG. 34. Enlarged view of syncytium *x*, in Fig. 36; showing the unequal size of the nuclei.

FIG. 35. *a* and *c*, surface nuclei in akinetic division from an egg in the same stage as Fig. 36; *b*, serosa nucleus in akinesis from a much older egg.

FIG. 36. Surface view of an egg shortly after the nuclei have begun to appear on its surface. *c*, cephalic end; *s*, sinus; *v*, ventral surface; *dd*, dorsal surface; *x*, a group of nuclei like that seen in section at *a*, in Fig. 26.

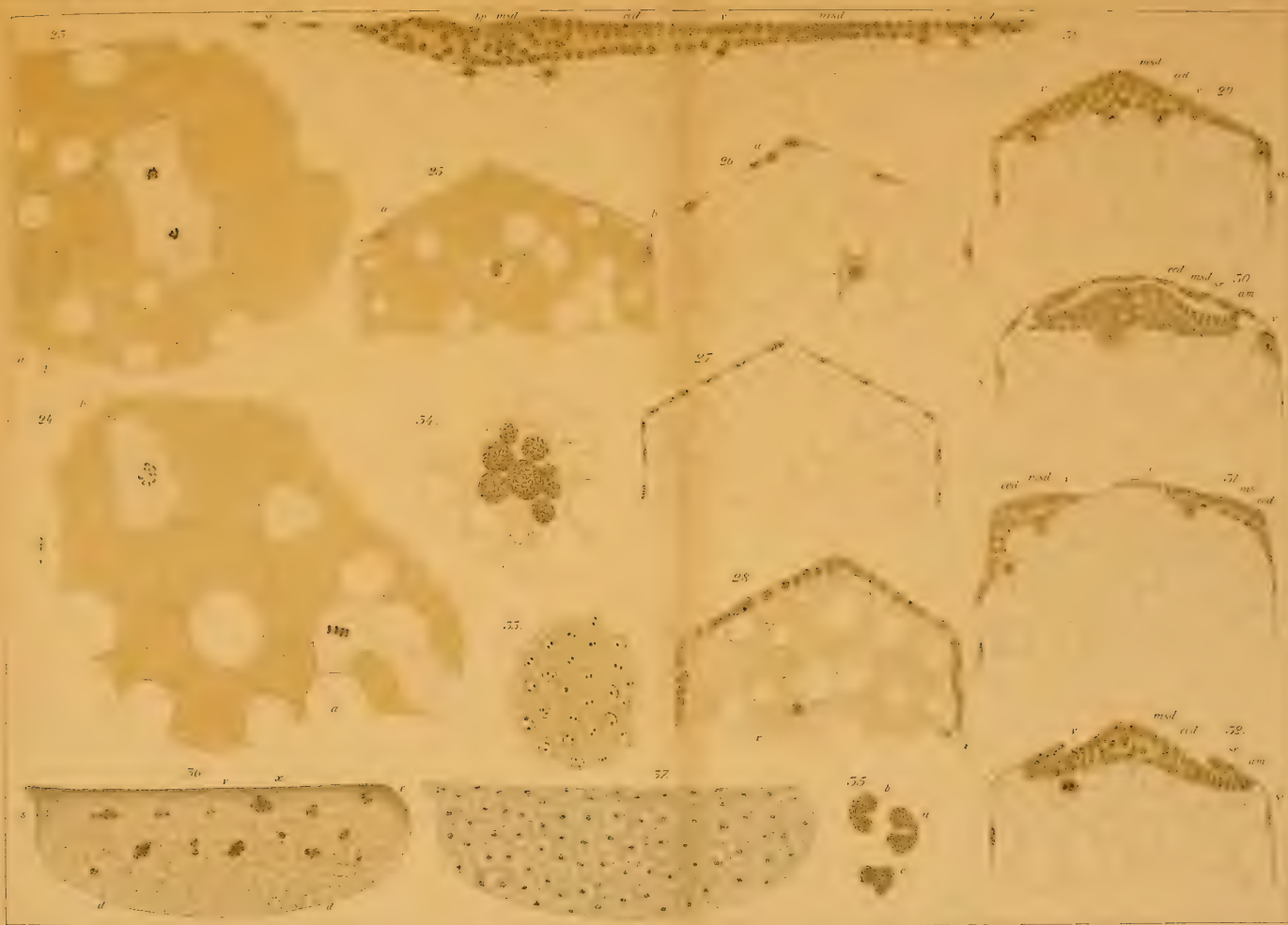
FIG. 37. Surface view of an egg in the blastema stage; 4 days old.

FIG. 38. Long. sect. along the carina *cn*, of Fig. 41; through the depression *bp*. *sr*, serosa; *bp*, depression; *ecd*, ectoderm; *msd*, mesoderm; *v*, yolk-cells.















## DESCRIPTION OF PLATE XVII.

*Blatta germanica.*

FIG. 39. Diagram of a median longitudinal section of an egg to show paths of nuclei. Explanation in the text.

FIG. 40. Diagram of a transverse equatorial section of an egg to show paths of nuclei. Explanation in the text.

FIG. 41. Surface view of the ventral face of an egg  $7\frac{1}{2}$  days old. *cn*, carina; *pcl*, beginnings of procephalic lobes; *bp*, depression (blastopore?) in the middle of the rounded area of proliferation.

FIG. 42. Surface view of the ventral face of an egg 8 days old. *as*, amnion and serosa beginning; *pcl*, beginning of procephalic lobes.

FIG. 43. Surface view of an embryo in "slipper" stage. *as*, amnion and serosa.

FIG. 44. Surface view of an embryo in the "hammer" stage,  $9\frac{3}{4}$  days old. *o*, opening in amnion and serosa over the oral region; *al*, antennary lobe; *p*, beginning of the second thoracic appendage.

FIG. 45. Embryo about 11 days old, isolated from the yolk. *lb*, labrum; *st*, stomodæum; *egl*, brain; *al*, antennary lobe; *md*, mandible; *mx*<sup>1</sup>, *mx*<sup>2</sup>, 1st and 2d maxillæ; *p*<sup>1</sup> to *p*<sup>3</sup>, thoracic appendages; *as*, amnion and serosa; *cp**l*, caudal plate.

FIG. 46. Embryo just after rupture of amnion and serosa; about 14 days old. *b*, cephalic end of yolk; *oc*, eye; *ad*, fat body; *ast*, anal stylets; *p*<sup>4</sup>, appendages of 1st abdominal segment; remaining references same as in Fig. 45.

FIG. 47. Front view of same embryo. References the same as in Fig. 45.

FIG. 48. Embryo almost ready to hatch. *oc*, eye; *egl*, brain; *gl*<sup>2</sup>, infraesophageal ganglion; *gl*<sup>3</sup> to *gl*<sup>5</sup>, the three thoracic ganglia; *gl*<sup>1</sup>, last of the abdominal ganglia; *oe*, oesophagus; *c*, crop; *gz*, gizzard; *ht*, heart; *st*, stomach; *rect*, rectum; *m**pg*, Malpighian vessels; *ast*, anal stylets; *y*, yolk; *lb*, labrum; *md*, mandibles; *mx*<sup>1</sup> and *mx*<sup>2</sup>, 1st and 2d maxillæ; *p*<sup>1</sup> to *p*<sup>3</sup>, thoracic appendages; *at*, antennæ.

FIG. 49. *Blatta germanica* about a day after hatching.

FIG. 50. Sagittal longitudinal section through the middle of the dorsal organ from an embryo 16 days old. *a*, anterior; *b*, posterior end of dorsal organ; *o*, depression; *v*, a yolk nucleus.

FIG. 51. Frontal section through the anterior end of dorsal organ in an embryo 18 days old. *cc*, heart; *nn*, nuclei of serosa cells; *o*, cavity formed from the depression *o*, of Fig. 50; *v*, yolk nucleus.

FIG. 52. Cross-section through the dorsum of an embryo to show formation of the heart. *h*, cavity of heart; *cb* *cb*, cardioblasts; *ecd*, ectoderm; *sm*, somatic mesoderm; *slm*, splanchnic mesoderm; *ent*, entoderm; *bl*, blood corpuscle becoming loosened from the wall of the heart; *y*, yolk.

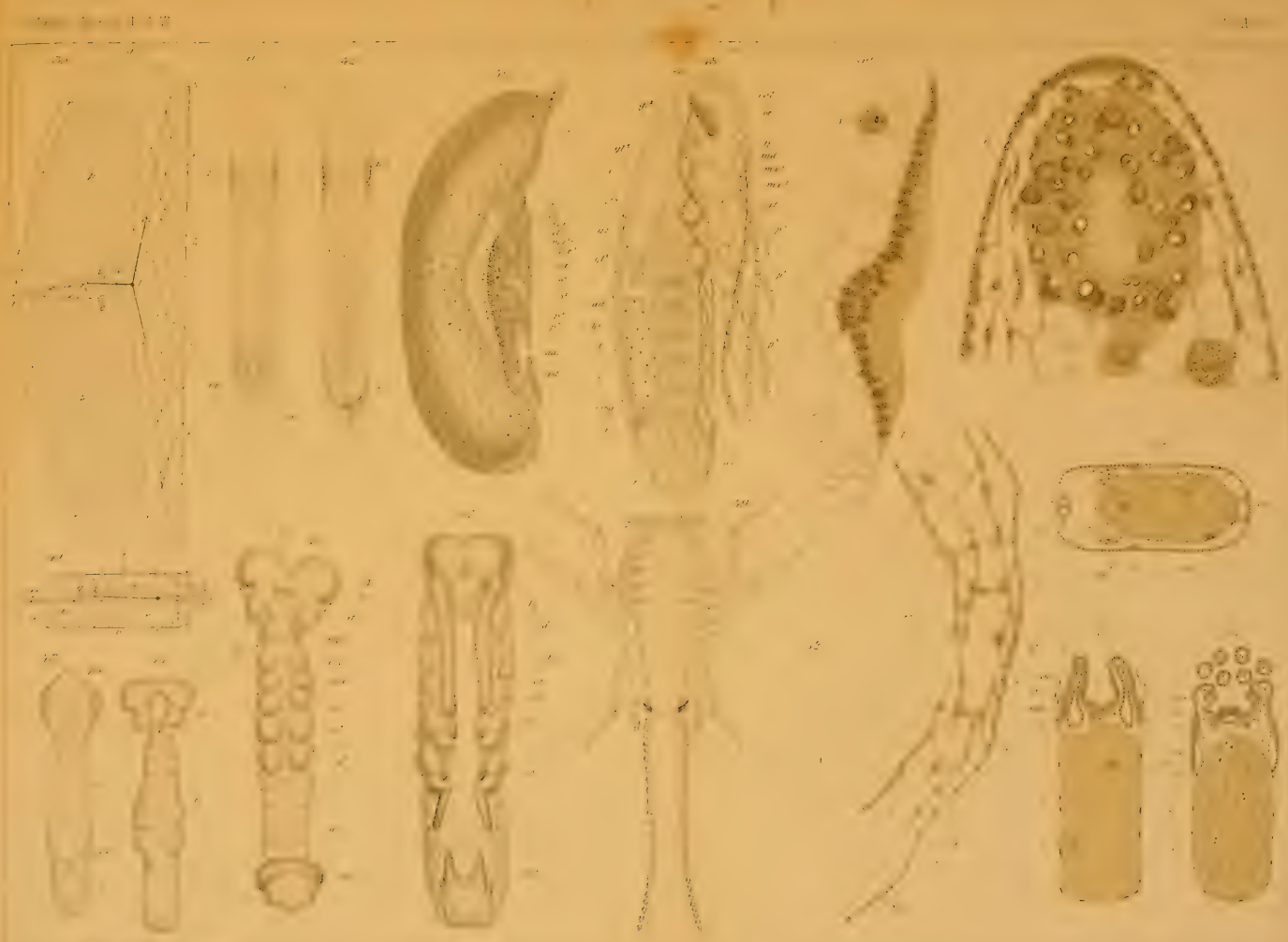
FIG. 53. Cross-section through the thorax of an embryo 12 days old. *nr*, neural thickening; *am*, amnion; *sr*, serosa; *v*, yolk nucleus; *msd*, mesoderm; *cl*, coelomic cavity; *p*<sup>2</sup>, second pair of legs.

FIG. 54. Cross-section through 2d maxillæ of an embryo 16 days old. *mx*<sup>2</sup>, second maxilla; *g*, duct of salivary gland; *y*, yolk; *ent*, entoderm; *cb*, cardioblast cells; remainder of references as in Fig. 53.

FIG. 55. Cross-section through the basal abdominal somite of an embryo 26 days old. *gl*, ganglion; *ad*, corpus adiposum; *v*, yolk nucleus; *tr*, tracheal opening; *y*, yolk; *cc*, heart.













## DESCRIPTION OF PLATE XVIII.

*Doryphora decemlineata.*

FIG. 56. Portion of a longitudinal section through a young egg shortly after the germinal vesicle has reached the periphery. *pl*, karyoplasm; *tr*, protoplasmic trabeculae connecting the karyoplasm with the intervittelline protoplasm (cytoplasm of the large cell which the egg represents); *y*, yolk bodies; *ep*, follicular epithelium; *nl*, germinal spot (nucleolus); *mb*, maturation balls (Reifungsballen of Stuhlmann) Zeiss  $\frac{1}{12}$ , oc. III.

FIG. 57. Section corresponding to that of Fig. 56 from an egg almost mature. *n*, large mass of chromatin destined to enter into the first polar spindle; *bl*, layer of surface protoplasm; *y*, yolk bodies; *ep*, follicular epithelium. Zeiss  $\frac{1}{12}$ , oc. III.

FIG. 58. Longitudinal section of a mature egg. *n*, resting nucleus originating from the mass of nuclein *n* of Fig. 57; *bl*, differentiated peripheral layer of protoplasm; *y*, yolk bodies; *v*, vitelline membrane; *ch*, chorion. Zeiss  $\frac{1}{12}$ , oc. III.

FIG. 59. Portion of median transverse section of a mature egg. *n*, first polar spindle in metakinetic stage; remaining references the same as in Fig. 58. Zeiss  $\frac{1}{12}$ , oc. III.

FIG. 60. Same section as in Fig. 59 of an egg about to be deposited, nucleus in last stages of anaphasis; the peripheral mass *p*<sup>1</sup> the first polar globule. Remaining references the same as in Fig. 58. Zeiss  $\frac{1}{12}$ , oc. III.

FIG. 61. Half of the median transverse section of an egg containing several nuclei *n*<sup>1</sup>, *n*<sup>3</sup>, none of which have as yet entered the surface layer of protoplasm *bl*. *y*, yolk.

FIG. 62. Half of the median transverse section of an egg shortly before the blastoderm stage. *v*, yolk-cells; *a*, blastema cell resting; *b*, blastema cells in metakinesis; *c*, blastema cells in anaphasis; *y*, yolk.

FIG. 63. Half of the median transverse section of an egg in the blastoderm stage. *v*, yolk-cells; *bld*, blastoderm.

FIG. 64. Half of a median transverse section of the egg of Fig. 67. *g*, half of the gastrular groove forming on the ventral face; *r*, ridge separating the groove from the remainder of the blastoderm; *p*, flat blastoderm cells on the dorsal surface of the egg.

FIG. 65. Median transverse section of an egg carrying the embryo represented in Fig. 71. The upper half of the section passes through *p*<sup>3</sup> of Fig. 71, the lower half a little in front of *x*. *sr*, serosa; *am*, amnion; *ecd*, ectoderm; *msd*, mesoderm; *ent*, cells still forming part of the induplicated ectoderm at *pl* which give rise to the entoderm; *y*, yolk.

FIG. 66. Ventral view of egg shortly after formation of blastoderm; the two parenthesis-shaped ridges inclose the portion which will sink in to form the gastrula.

FIG. 67. Ventral view of egg with gastrula more advanced. *a*, oral spade-shaped broadening of the gastrula; *b*, the point at which the groove turns abruptly inwards; *sr*, serosa.

FIG. 68. Lateral view of same egg. *pcl*, procephalic lobes; remaining references the same as in Fig. 67.

FIG. 69. Caudal end of egg represented in Fig. 70. *g*, gastrula; *am*, caudal fold of the amnion; *sr*, serosa.

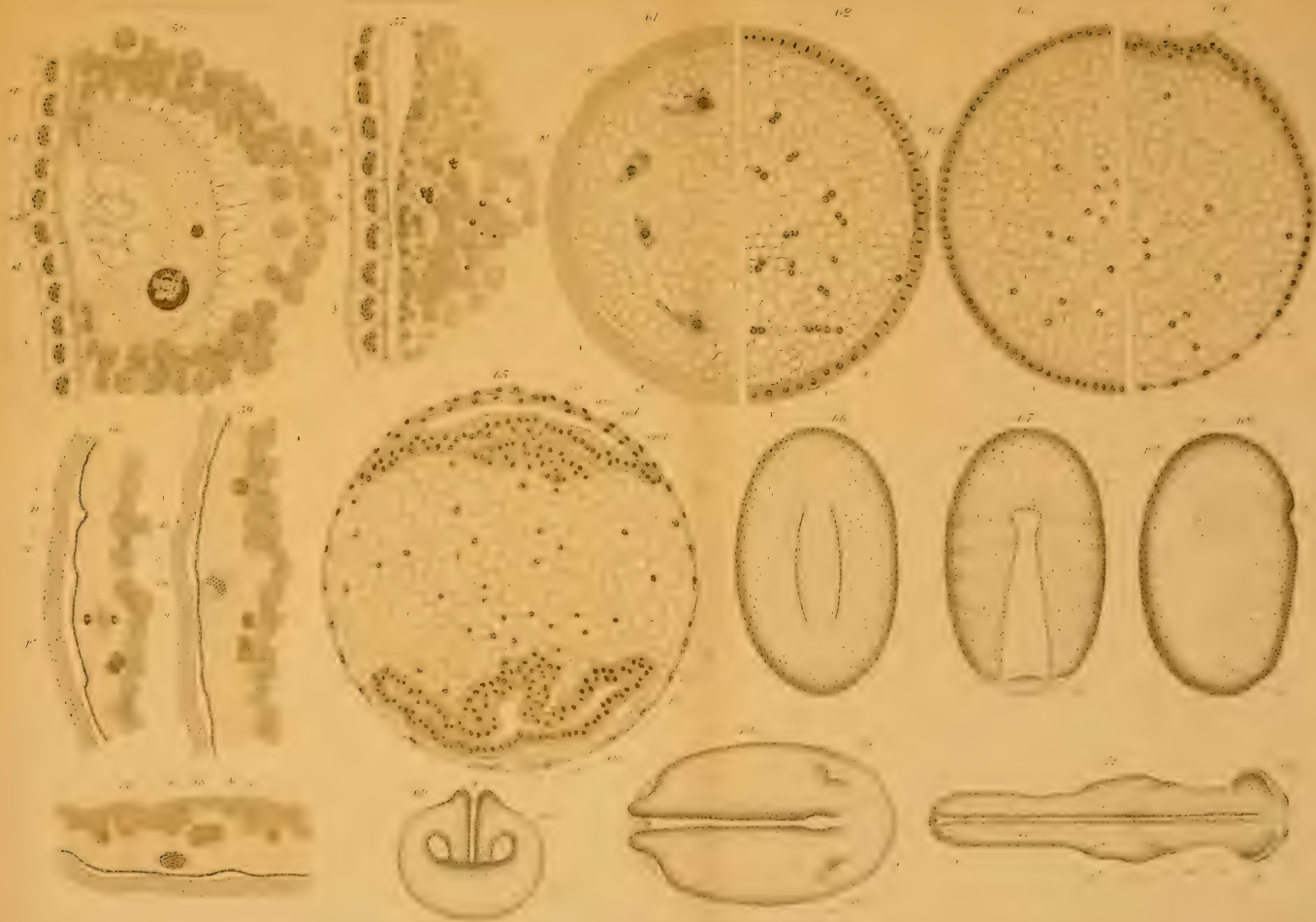
FIG. 70. Ventral view of an egg with gastrula fully formed. *a*, oral widening of the gastrula; *am*, cephalic fold of amnion; *br*, brain thickening.

FIG. 71. Slipper-shaped embryo removed from egg and unrolled. *p*<sup>1</sup> to *p*<sup>3</sup>, indications of the 3 pairs of thoracic appendages; *as*, amnion and serosa; *am*, cephalic fold of amnion and serosa; *a*, oral and *x*, anal end of gastrula; *b*, maxillary region.















## DESCRIPTION OF PLATE XIX.

*Doryphora decemlineata.*

FIG. 72. Embryo shortly after the appearance of the appendages, unrolled and isolated. *o*, stomodæum; *a*, proctodæum; *lb*, labrum;  $b^1$  to  $b^3$ , three brain segments;  $og^1$  to  $og^3$ , three segments of the optic ganglion;  $op^1$  to  $op^3$ , three segments of the optic plate;  $t^1$  to  $t^5$ , five pairs of invaginations which form the tentorium;  $t^1$  to  $t^{20}$ , tracheal invaginations; the two last pairs  $t^{19}$  and  $t^{20}$ , either disappear or form the openings of the sexual ducts; *at*, antennæ; *md*, mandibles;  $mx^1$  and  $mx^2$ , first and second maxillæ;  $p^1$  to  $p^3$ , three pairs of thoracic appendages; *c*, commissure connecting the two ganglionic thickenings  $g^1$  of the intercalary segment;  $gl$ , ganglionic thickening; *mst*, Mittelstrang thickening;  $mpg^1$  to  $mpg^3$ , three Malpighian vessels.

FIG. 73. Embryo just after the closing of the amnion and serosa (*sr*) unrolled and isolated. *a*, oral, *x*, anal end of the gastrula; *pcl*, procephalic lobe;  $mx^2$ , second maxilla;  $p^1$  to  $p^3$ , three thoracic appendages; *cp*, caudal plate.

FIG. 74. Ventral view of embryo, the lateral walls of which have embraced half the yolk; references same as in Fig. 72.

FIG. 75. Lateral view of embryo ready to hatch. *at*, antenna;  $t^8$ , mesothoracic spiracle;  $t^{10}$  to  $t^{18}$ , abdominal spiracles; *hsp*, first hatching-spine.

FIG. 76. Sagittal section to one side of the median line through the tail of embryo, Fig. 72. *am*, amnion; *sr*, serosa;  $mpg^1$  and  $mpg^3$ , first and third Malpighian vessels; *ecd*, ectoderm; *msd*, mesoderm; *ent*, forward growing band of entoderm; *ent<sup>l</sup>*, mass of entoderm left under the end of the proctodæum.

FIG. 77. Transverse section through the second pair of Malpighian vessels ( $mpg^2$ ) of the same embryo. *x*, proctodæum; other references same as in Fig. 76.

FIG. 78. Median cross-section through an egg containing an embryo a little older than that represented in Fig. 72. The section cuts the embryo at two places. That with the entoderm (*ent*) belongs to one of the last abdominal segments, that without entoderm to one of the basal abdominal segments. *nr*, neural thickenings; *ecd* and *ent*, ectoderm and entoderm; *slm*, *sm*, splanchnic and somatic mesoderm, inclosing the coelomic cavity; *cb*, *cb*, cardioblast cells.

FIG. 79. Cross-section through the middle of the proctodæum of an embryo somewhat younger than that represented in Fig. 74. *x*, proctodæal cavity; *cl*, coelomic cavity; *gl*, ganglion; *mst*, Mittelstrang;  $mpg^1$  to  $mpg^3$ , Malpighian vessels surrounded by mesodermic elements.

FIG. 80. Cross-sections through the sexual orifices of an embryo in the stage of Fig. 74. *go*, *go*, openings of efferent ducts; remaining references as in preceding figures.

FIG. 81. Surface view of two eyes (corresponding to eyes V. and VI. of *Acilius* as described by Patten). *n*, large nucleus in the centre of each eye.

FIG. 82. Median sagittal section through an embryo in about the stage represented in Fig. 73. *am* and *sr*, amnion and serosa; *o*, point at which the anterior end of the embryo passes into the amnion; *p*, point at which the posterior end passes into the amnion; *st*, stomodæal depression; *x*, point near which the proctodæum will appear;  $pl^1$ ,  $pl^2$ , anterior and posterior thickenings of the inner layer; from which the entoderm, *ent<sup>1</sup>*, *ent<sup>2</sup>*, originate. *msd*, mesoderm;  $mx^1$  and  $mx^2$ , first and second maxillæ;  $p^1$  to  $p^3$ , legs; *c*, cells which entered the amniotic cavity. Under the two thickenings  $pl^1$ ,  $pl^2$ , are seen the peculiar degenerating nuclei passing into the yolk, which has become segmented.













## DESCRIPTION OF PLATE XX.

*Doryphora decemlineata.*

FIG. 83. Portion of cross-section through a basal abdominal segment of an embryo somewhat younger than that represented in Fig. 74. *am*, amnion; *ent*, entoderm; *ect*, ectoderm; *tr*, tracheal invagination; *gl*, ganglion; *mst*, Mittelstrang; *sm*, somatic mesoderm; *slm*, splanchnic mesoderm; *cb*, cardioblasts.

FIG. 84. Transverse section through middle of abdomen of embryo, Fig. 74. *gn*, sexual organ; *mpg*, Malpighian vessel; remaining references same as in Fig. 83.

FIG. 85. Cross-section through metathoracic segment of an embryo considerably older than Fig. 74. *ln*, lateral nerve trunk; *ap*, appendage; *sr*, serosa; *ad*, fat cells; *a*, amnion cells entering the yolk at *b*; remaining letters the same as in Fig. 83.

FIG. 86. Cross-section through mesothorax of an embryo after the formation of the heart, *ht*. *hsp*, thickening of ectoderm which secretes the metathoracic hatching-spine; *cl*, first cuticle shed by the embryo; *cm*, longitudinal commissures between two thoracic ganglia; *f*, furca; *r*, point of attachment of muscles to the furca; *msl*, muscular tissue; remaining letters as in preceding figures.

FIG. 87. Cross-section through caudal plate of embryo before the closure of the anal end of the gastrula. *x*, *c*, cell about to wander through the blastopore into the amniotic cavity; *msd*, mass of cells which will form the mesoderm as soon as the blastopore closes; *ent*, cells imperfectly differentiated from those of the mass, *msd*, which are to give rise to the entoderm; *v*, yolk nucleus; *am*, amnion; *sr*, serosa.

FIG. 88. Cross-section, more highly magnified than the preceding, through the caudal plate of an embryo somewhat younger than that of Fig. 73. The blastopore has closed, and the depression *x* marks the beginning of the proctodæal invagination; *l* is the line, unusually distinct in the section figured, separating the mass of mesoderm cells (*msd*) above it from the smaller mass of entoderm cells (*ent*) below it; *l*, *o*, *v*, degenerating nuclei which pass from the entoderm into the yolk; *y*, yolk nucleus.

FIG. 89. Frontal section through the cardioblasts (*cb*) of an embryo in the same stage as Fig. 84; *cb*, row of cardioblasts; *ecd*, *msd*, *ent*, germ layers; *ad*, fat cells.

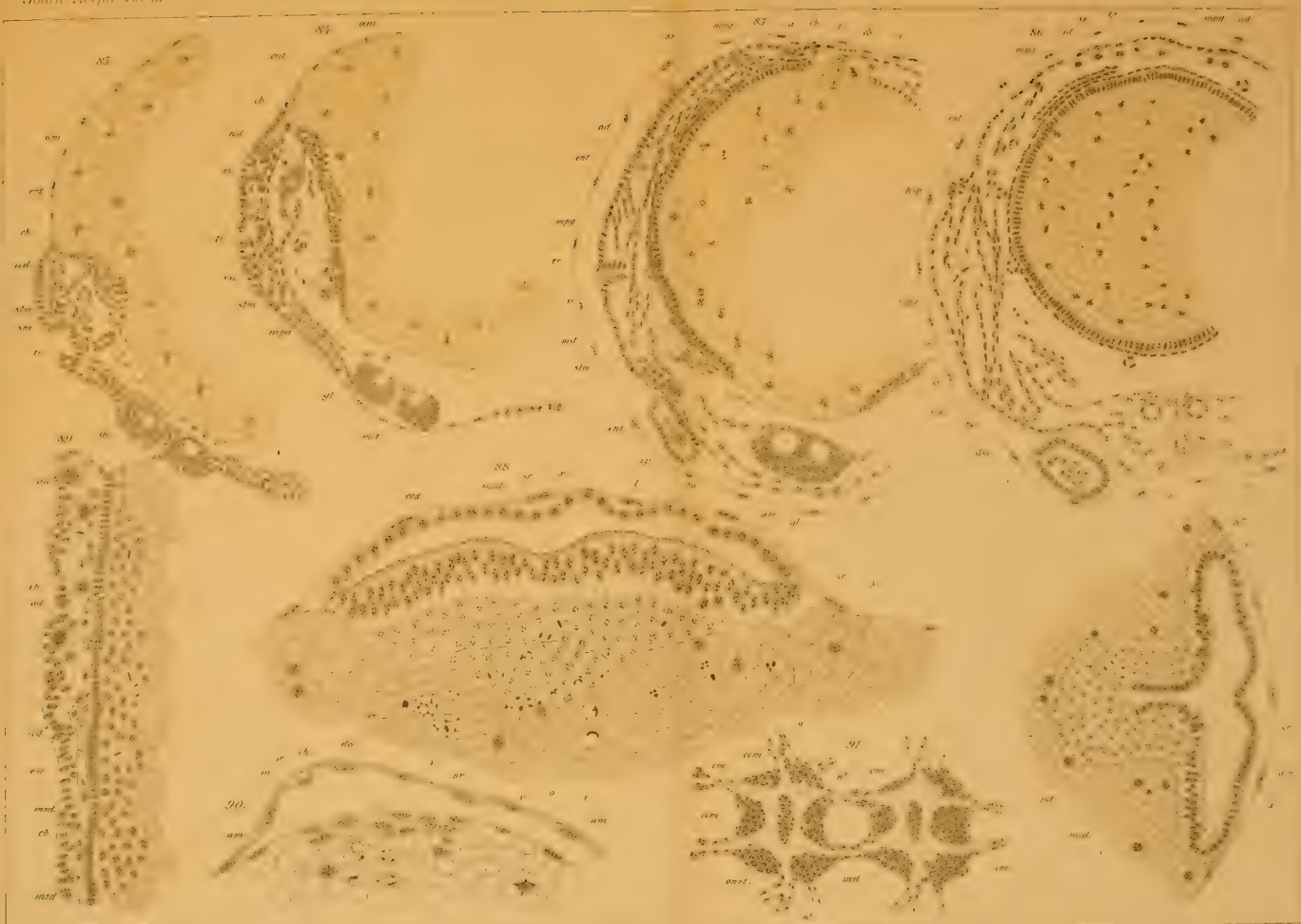
FIG. 90. Portion of a cross-section through the lower part of the dorsal yolk of an embryo in the stage of Fig. 74. *ch*, chorion; *sr*, serosa; *am*, amnion; *do*, amniotic dorsal organ; *m*, amniotic nuclei degenerating; *v*, yolk nucleus.

FIG. 91. Frontal section through the meso- and meta-thoracic ganglia of the embryo, Fig. 74. *cm*, longitudinal commissures; *ccm*, cross-commissures; *n*<sup>1</sup>, anterior nerve trunk; *n*<sup>2</sup>, posterior nerve trunk; *onrl*, outer neurilemma; *inrl*, inner neurilemma.















## DESCRIPTION OF PLATE XXI.

*Doryphora decemlineata.*

FIG. 92. Sagittal section through stomodæum (*st*) of an embryo in the same stage as Fig. 72. *ecd*, *ent*, *msd*, germ layers; *lb*, labrum.

FIG. 93. Cross-section of median dorsal portion of an embryo, just after the union of the ectoderm (*ecd*) from either side of the body; *cb*, cardioblasts; *ad*, fat cells; *am*, one of the last amnion cells passing into the yolk through the opening between the two lateral halves of the mesenteron. *msl*, muscular tissue; *ent*, entoderm; *slm*, splanchnic mesoderm.

FIGS. 94 to 104. Sections 1, 3 to 8, 10, 11, 13, and 14, through the mesothoracic ganglion of an embryo somewhat younger than that of Fig. 74. *cm*, longitudinal commissure; *ccm*, cross-commissures; *ps*, Punktsubstanz; *mst*, Mittelstrang; *ecd* and *e*, hypodermis; *gbl*, ganglioblasts.

FIG. 105. Section through fore part of metathoracic ganglion. The Mittelstrang, *mst*, persists as the *furca* (subsequently chitinous). *gl*, ganglion; *ps*, Punktsubstanz; *msl*, muscular tissue attached to the furca; *ecd*, hypodermis.





# JOURNAL OF MORPHOLOGY.

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## THE EMBRYOLOGY OF THE EARTHWORM.

EDMUND B. WILSON.

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## PART I. — INTRODUCTORY.

I. THE following paper contains the results of an examination of the development of the earthworm that has occupied my attention at intervals for a considerable time. I shall not attempt to give an exhaustive account of the development, and I must leave unsolved a number of important problems, some of which can perhaps only be fully elucidated by the study of other and more favorable material. The results already attained differ widely, however, from generally accepted views in respect to many important phenomena and clearly show the need for a re-examination of many features of annelid development, even in the case of forms that have already been carefully studied.

It is hardly necessary to call attention to the historical importance of Kowalevsky's pioneer researches on the embryology of *Lumbricus* and *Euaxes* (No. 27), or to the interest of the questions suggested by Kleinenberg's later and more detailed studies (No. 28). Both these works have played an important part in the advance of comparative embryology, and must always command the admiration of morphologists. Both were nevertheless far from exhaustive; and later investigations have left our knowledge of the subject not only incomplete, but as I shall endeavor to show in the sequel, obscured by a false conception of some of the most important phenomena of development.

The more important results of my work may be briefly summarized as follows:—

(1) The cleavage is unequal and variable, and results in the formation of a blastula containing a large blastocœl. The gastrula is formed by embolic invagination. The blastopore, which at first occupies the entire ventral surface, narrows to a slit-like form, its longer axis coinciding with the long axis of the adult body; it then closes from behind forwards, its foremost portion persisting as the mouth. The germ-bands are already established at the time of the invagination and lie at the sides

of the primitive blastopore. They are from the outset united in the middle line behind the posterior lip of the blastopore, but remain separate in front until the establishment of the mouth, when they extend forward, join in the median dorsal line, and thus form a complete longitudinal ring surrounding the region of the primitive blastopore.

(2) The entire mesoblast is derived from a pair of primary mesoblasts or teloblasts that lie at the posterior ends of the germ-bands, and no mesoblastic elements arise from the ectoblast overlying the germ-bands. The primary mesoblasts are differentiated in the course of the cleavage and are pushed into the segmentation-cavity some time before the beginning of gastrulation, in the manner described by Kleinenberg (No. 28). The cells formed by the continued proliferation of these primary mesoblasts are at a very early period differentiated into two groups which, though having a common origin and remaining in continuity, may conveniently be designated by different terms.

The cells of the first group have histologically the character of mesothelium, form the mesoblastic parts of the germ-bands in the trunk region, and enclose the paired cœlomic cavities. They may therefore be called collectively the *trunk-mesoblast*. The cells of the second group arise by migration from the dorsal and anterior parts of the germ-bands, and may therefore be called the *migratory mesoblast*. They have histologically the character of mesenchyme, and form a nearly complete investment of the body in the trunk region, but also extend forward to form the cephalic mesoblast of the præoral lobe or prostomium. [It should be clearly understood that this distinction is made solely for the sake of convenient description, and that all the cells of both groups arise from the two primary mesoblasts and from no other source.]

(3) When fully established the germ-bands consist of three strata of cells, as in Hirudinea, namely: (*a*) an outer stratum (ectoblast), one cell in thickness, which arises directly from the original outer layer of the gastrula, and persists as the hypodermis; (*b*) an inner stratum (mesoblast) consisting of granular cells derived from the two primary mesoblasts; from it arise the muscles, dissepiments, blood-vessels, peritoneal epithelium, reproductive organs, and the inner part of the nephridia; (*c*) a

middle stratum which lies between (*a*) and (*b*) and agrees in general histological character with the ectoblast (from which it is indirectly derived). From the middle stratum arise (*a*) the nervous system, (*b*) the outer part of the nephridia, (*c*) the setigerous glands and the setæ.

(4) The middle stratum is arranged in a series of distinct longitudinal cell-rows which, in early stages, lie at the surface and form part of the general ectoblast, but afterwards sink below the surface and are completely covered by the remaining ectoblast. Of these rows there are either three or four in each germ-band. The inner (or ventral) row gives rise to the corresponding half of the nervous system, and will therefore be called the *neural row*, or *cord*. The two succeeding rows on each side give rise to a portion of the nephridia and to the inner series of setigerous glands, and will be called the *nephritic rows*. The fourth or outer row, which I have found as a distinct structure in one species only, gives rise to cells which form the outer or dorsal part of the middle stratum. Their precise fate is still in some doubt, but it is probable that they give rise to the outer series of setigerous glands, though perhaps to other structures as well.

(5) Until a comparatively late stage each row of the middle stratum terminates behind in a large cell (teloblast), which is the parent of the entire row, and thus of all the structures to which the row gives rise. The inner teloblast will therefore be called the *neuroblast*, those at the ends of the nephritic rows the *nephroblasts*; the fourth, owing to the uncertainty of its fate, will be called the *lateral* or *outer teloblast*. These four teloblasts may be called the *anterior teloblasts* to distinguish them from the posterior or mesoblastic teloblasts which lie at the extreme hinder ends of the germ-bands.

(6) The teloblasts of the middle stratum are at first ordinary ectoblast cells which cannot be distinguished from the adjoining cells. They first appear shortly after the completion of gastrulation, and at this time lie at the surface, like the rows (now very short) to which they give rise. At a later period they sink below the surface and ultimately break up into groups of cells lying at the hinder ends of the corresponding rows.

(7) The cephalic lobe (prostomium) arises by the union of the anterior ends of the germ-bands. The mesoblastic part

arises by the forward growth and union in the median line of the mesoblastic bands, a process which is effected by proliferation and migration of the mesoblast cells already formed, and not by the formation of new mesoblastic elements from the superjacent ectoblast. The prostomial cavity is from the very first unpaired.

(8) The præoral or cephalic ganglia are differentiated out of the front ends of the neural rows at a time when these rows are fused with the ectoblast, and before they have met in the median line in front of the mouth. There is therefore no median apical plate (Scheitelplatte), but only a pair of lateral ectoblastic thickenings continuous behind with the neural rows. I am unable to say positively whether the cephalic ganglia actually arise from the neuroblasts, but I believe they do not [p. 416].

For more special accounts of the origin and differentiation of the layers and the detailed development of organs, the reader is referred to Part II. It is, however, desirable to preface the special descriptions with a short discussion of their relation to the work of other investigators.

The principal questions suggested by my work relate to the origin of the mesoblast and the history of the middle stratum of the germ-bands. The existence of this stratum in the germ-bands of *Oligochaeta* has not hitherto been distinctly recognized, though Kowalevsky and Kleinenberg indicate it in their figures of *Lumbricus*. The nephric and outer cell-rows and the four anterior teloblasts have hitherto been observed only in the *Hirudinea* and adequately studied only in the single case of *Clepsine*. As regards the mesoblast, I am fully convinced that the whole of the "epiblastic mesoblast" which Kleinenberg believed to be derived directly from the outer layer, is simply the middle stratum which he failed to distinguish from the inner or mesoblastic stratum. This misinterpretation has importance because of the emphasis which Balfour placed upon Kleinenberg's conclusions, and still more on account of its connection with the views put forward in Kleinenberg's recent remarkable paper on *Lopadorhynchus* (No. 31). In this masterly work the author not only rejects the ordinary conception of the mesoblast, but even goes so far as to deny its existence as a primary feature of development, all "mesoblastic" structures being conceived as direct or indirect derivatives of the two primary layers, ectoblast or



entoblast, which alone are of fundamental significance. Without presuming to question the justness of these conclusions, which are certain to exercise an important influence on embryology, I wish to point out the fact that Kleinenberg's views appear to have been influenced in a measure by his conclusions in respect to the origin of the "mesoblast" in *Lumbricus*, and that these conclusions are certainly erroneous. In his paper on the development of the earthworm Kleinenberg obviously means that the layer of cells ordinarily called "mesoblast" in this animal—that is, the layer of undifferentiated cells from which the muscles, blood-vessels, dissepiments, peritoneal epithelium, and reproductive elements arise—has a double origin, part arising from the primary mesoblasts at the posterior ends of the germ-bands, but a greater part being directly derived by proliferation of the overlying ectoblast. But after the most careful study of the question by means of complete series of sections of all stages of development, I can assert positively that this is not the case. It is true that new elements are added to the germ-bands from the ectoblast; it is not true that these elements assume the character of mesoblastic cells and give rise to structures ordinarily recognized as mesoblastic. On the contrary, they are from first to last ectoblastic structures in the sense of being derived from the outer layer of the gastrula long after the layers are completely established, in retaining the histological characteristics of the ectoblast, in remaining long embedded in that layer, and in giving rise to structures (nervous system, setigerous glands) that in other forms are unquestionably of ectoblastic origin; and it would lead to hopeless confusion in the use of terms to regard the middle stratum as forming a part of the "mesoblast," taking the word in the sense employed by Kleinenberg in his paper on *Lumbricus*. It is furthermore perfectly clear that the middle stratum of *Lumbricus* in no way represents that part of the "mesoblast" (using the word in the ordinary sense) that is split off from the ectoblast in *Lopadorhynchus* (e.g. the muscle-plates), for there can be no question that the muscles, dissepiments, vessels, peritoneal epithelium, reproductive organs, and a part of the nephridia, are derived from the inner or mesoblastic stratum, and hence ultimately from the two primary mesoblasts.

This preliminary explanation will, I trust, make plain in what

respect, apart from all differences of terminology, my views differ from those of Kleinenberg, and will prevent confusion in the use of terms. I may add lastly that some of my conclusions, especially those relating to the origin of the nephridia, have been criticised by a number of writers, notably by Bergh (No. 8), whose remarks are, however, couched in such terms as to render a reply unnecessary. A careful re-examination of the whole subject has not essentially altered my original view, though I am ready to admit having perhaps been somewhat too positive in my statements as to the origin of the nephridia. I trust that the present paper will at least present clearly the evidence on which my conclusions were based.

## PART II. — DESCRIPTIVE.

I have examined the development of three species to which I shall refer respectively as *Lumbricus terrestris*, *L. communis*, and *L. fetidus*, though the latter two forms are placed by most recent writers in the genus *Allolobophora*, and the specific name *communis* has been discarded.<sup>1</sup>

The three species agree closely in the general outlines of their development, as far as I have been able to follow them,

<sup>1</sup>Vejdovsky [No. 44] gives the following names to these species; I add also a partial synonymy, as given by the same author, which will suffice to identify the forms I have studied.

1. *Lumbricus terrestris* L., = *L. agricola* Hoffmeister.
2. *Allolobophora cyanea*, = *Enterion cyaneum* Sav., = *Lumbricus communis cyaneus* Hoffm., = *Allolobophora turgida* Eisen.
3. *Allolobophora fetida* Eisen = *Enterion fetidum* Sav., = *Lumbricus fetidus* Dugès, = *L. olidus* Hoffm.

According to Vejdovsky the form studied by Kleinenberg has the following synonymy:—

*Allolobophora carnea*, = *Enterion carneum* Sav., = *Lumbricus trapezoides* Dug., = *L. communis carneus* Hoffm., = *Allolobophora mucosa* Eisen.

Ude, however, accepts Eisen's names for the two species included under Hoffmeister's "*L. communis*," and in view of this disagreement I have preferred to use the specific name *communis*. I prefer to apply the generic term *Lumbricus* to the three species I have studied, partly for the sake of brevity, but more especially because Eisen's division of the earlier genus *Lumbricus* into *Allolobophora* and "*Lumbricus*" is based upon a trifling anatomical distinction which does not correspond to the differences I have observed in the mode of development—*i.e.*, the two species of "*Allolobophora*" (*L. communis* and *L. fetidus*) differ somewhat in development, and one of them agrees precisely with *L. terrestris*, which is a typical "*Lumbricus*" in Eisen's sense.

though they differ in some interesting details. I have relied mainly upon *L. fætibus* for the early stages, but *L. communis* and *L. terrestris* are much better adapted for the later development, since in *L. fætibus* the albumen becomes so hard as to render section cutting well-nigh impossible without removal of the contents of the archenteron. I have also examined embryos of a species of small fresh-water Oligochæte (see Figs. 55, 56) which I have been unable to identify with the adult form.

## II. EGG-LAYING, ETC.

In spite of many individual variations, the egg-capsules of the various species of *Lumbricus* are, as a rule, readily distinguishable in form, color, and size. Those of *L. fætibus*, which are laid in and about manure-heaps, are rather regularly fusiform, varying in color from light yellowish to dark brownish olive; they measure on the average about 4-6 by 2-3 millimeters. The albumen is tough and jelly-like, dissolves with difficulty in water, and becomes of a horn-like consistency after the hardening action of reagents. Each capsule contains from ten to sixty ova, of which not more than ten or twelve undergo development, and this number may be reduced to one or two, particularly in the winter season. The capsules of *L. communis* and *L. terrestris* are deposited in earth, usually a few inches below the surface. Those of the first species are irregularly fusiform, and of a brighter yellow color than those of *L. fætibus*; they measure on the average about 5-7 by 3-5 millimeters. Those of *L. terrestris* are still larger (mean measurements are 6-8 by 4-6 mm.), regularly fusiform, but more swollen and rounded than those of the other species; their color is a dark olive. In both species the albumen has a slimy, mucus-like consistency, and is not greatly hardened by reagents. In *L. terrestris* only one egg develops out of several included in the capsule. In *L. communis* two embryos are produced as a rule, and in many cases, though not in all, both arise as twins from a single ovum, as has been described by Kleinenberg.

Egg-laying seems in special cases to continue throughout the year, though it is most active in the spring and summer months. I have found the capsules of *L. fætibus* out-of-doors in nearly every month of the year, but in mid-winter they are only found

in decomposing compost-heaps where the temperature is maintained at a tolerably high point. The rate of development varies greatly, and depends not only upon the temperature, but also upon the vigor or other internal properties of the individual embryos, for in late stages the embryos in a single capsule are often found in very different stages of advancement. It is therefore impossible to determine the age of the embryo without following its actual development. In laboratory cultures the young worms usually make their escape from the capsule in about two or three weeks.

For the present I am obliged to pass over the phenomena relating to the maturation and fecundation of the ova, and my account of the cleavage will be found unsatisfactory, owing to the impossibility of following continuously the development of the individual ova. Development continues for some time after removal of the segmenting ova from the capsule, but pathological changes invariably supervene, however careful the treatment, and I am persuaded that no trustworthy results can be obtained by this method. After making numerous drawings of embryos thus studied, I rejected them all, and relied wholly on the comparative study of specimens examined or preserved immediately after opening the capsules. The results thus obtained, though based on the examination of a very large number of specimens, are necessarily incomplete; but I believe them to be trustworthy as far as they go.

As in so many other cases, periods of quiescence, or "resting stages," alternate with periods of division throughout the cleavage process. In the resting periods the cells are closely pressed together, and their outlines are often hard to see; so that it is well-nigh impossible to interpret some of the stages unless they are studied in the active period. Moreover, the cleavage process varies greatly in the order of division, which after the first two divisions loses all appearance of regularity. On account of these circumstances the segmenting ova vary widely in appearance, and the process of cleavage thus acquires that apparent irregularity which other observers have found so perplexing. It is now well known, however, that the segmenting ova of various other animals (*e.g.* Mollusca, Coelenterata) are likewise subject to considerable variation, which in some cases at any rate is due simply to temporary acceleration or retardation in the divisions



of individual cells (No. 53), and probably does not affect the essential character or the end-result of the cleavage. The following description applies to *L. fatidus*.

### III. CLEAVAGE.

1. The fertile ova are slightly ovoid in shape and measure about 0.125 mm. by 0.112 mm. They are surrounded by a delicate vitelline membrane which is at first closely applied to the vitellus, but afterwards enlarges so as to become widely separated from it. The vitellus is laden with small, clear yolk-spheres and granules, which only partially obscure its transparency and usually do not prevent a clear view of the interior of the embryo after suitable treatment with reagents. Several polar cells are formed, probably by the division of two primary polar cells directly separated from the ovum. They usually occur in two groups of three or four each (Figs. 1 and 2) which lie in the plane of the first cleavage, but appear afterwards to shift their position so that no constant relation between them and the embryo can be recognized. At the first cleavage the vitellus divides into two unequal parts, the plane of division passing through the polar cells (Fig. 2). The second cleavage divides the smaller cell into two nearly equal parts, and (as I believe) separates a third small cell from the larger of the first two (Figs. 3-5). No constant difference in the granulation of these four cells can be made out. In the ensuing resting stage a distinct cavity appears between the three smaller and the one larger cell, but this cavity disappears afterwards, and cannot be identified with the true blastocoel. I have occasionally seen apparently normal ova in which the four cells of this stage are nearly equal in size, and others in which only three cells were present. With the third cleavage normal variation certainly begins. As a rule, the largest of the four cells shown in Figs. 3-5 divides into two equal parts, and the three smaller cells lie in a group above the angle between them (Fig. 6). In some cases, however, only two small cells are present. In the next stage, as a rule, the number of small cells is increased to four (Fig. 7), probably by division of one of the smaller cells of the preceding stage, after which each of the large cells divides into two unequal parts (Figs. 8-14), the smaller of

which (3, 4) is intermediate in size between the four (or three) small (5, 6, 7) and the two (1, 2) largest cells. In some cases, however, the large cells undergo this division when only three small cells are present, as shown in Fig. 10. At the end of this period, therefore, the embryo consists of seven (Fig. 10), or eight (Figs. 12, 13), cells, namely: two large equal cells (1, 2, Figs. 10, 11), two middle-sized equal cells (3, 4), and three or four small cells (5, 6, 7, 8). The latter are probably situated at the upper or ectoblastic pole.

From this time forward the divisions cannot be followed in detail, but I do not believe that any definite order exists. When the embryo consists of not more than twelve or sixteen cells a large segmentation cavity appears, and the embryo becomes a blastula, the walls of which consist of a single layer of cells (Figs. 19, 20). At one pole these cells are smaller than at the other, but it is not possible to draw any definite line between micromeres and macromeres. The structure of the embryo at this period may be understood by a study of Figs. 15-19, which are accurate drawings of a single individual in several different positions, so that every cell may be seen. There are in all thirteen cells, which do not perceptibly differ in the character of the protoplasm, and I am unable to say what is the precise relation of these cells to those of earlier and later stages; or to recognize the future primary mesoblasts, though it is possible that they are already present.

*Comparative.*—From the foregoing account it will be seen not only that I have had no better success than Kleinenberg in following the details of the cleavage process, but that my results, as far as they go, do not fully coincide with his; and I can only reconcile the discrepancy by supposing that, aside from individual variation, there are some constant differences between *L. fætidus* and *L. "trapezoides."* The two-celled and four-celled stages appear to be essentially the same in these species; and the same is true of the three-celled stage, though it seems to occur more rarely in *L. fætidus*. Kleinenberg's six-celled stage corresponds closely with that shown in Fig. 7, but it would seem, from his description, to arise in a quite different manner. From this point to the full establishment of the blastula I am unable to correlate Kleinenberg's observations with my own.

A comparison of my figures with those of Whitman on *Clep-*

*sine* (No. 50), and Vejdovsky on *Rhynchelmis* (Nos. 45, 48), shows that it is impossible to establish any certain homology between these forms and *Lumbricus*. At first sight the four-celled stage shown in Fig. 3 might seem to correspond with that of *Rhynchelmis*, but the subsequent development fails to establish the comparison. The eight-celled stage (consisting of four macromeres and four micromeres), which may be taken as characteristic of the typical unequal cleavage, seems to have been entirely masked by secondary changes in the cleavage periods, and the facts are still too incompletely known to justify any speculation as to the history of these changes.

The one positive result that seems to be brought out by the comparison is that the phenomena of cleavage in *Lumbricus* are of a highly modified character, and this conclusion is also indicated by the individual variability of the segmenting ova. This conclusion, unsatisfactory as it is, may have an important bearing on the general interpretation of the process of gastrulation.

2. *Origin of the Layers.*—My observations on the origin of the primary mesoblasts agree closely with those of Kleinenberg, and show beyond all question that the mesoblast is differentiated long before the invagination of the gastrula.

The changes resulting in the formation of the blastula usually occupy from 18 to 24 hours. During the following 24 hours (more or less) the cells increase rapidly in number by radial divisions, the blastula remaining one-layered and nearly spherical. Two of the larger cells lying side by side near the equator of the blastula (Fig. 23) undergo no radial division, and their inner ends soon project into the blastocœl. The inner ends are then separated from the peripheral parts by tangential divisions, which take place nearly at the same time in the two cells. The two smaller cells thus formed lie side by side in the blastocœl, which they nearly or quite fill (Fig. 25). The two larger cells, which still lie at the surface of the blastula, are the "primary mesoblasts," which by continued divisions give rise to the entire mesoblast. I have failed to trace the origin of these cells in the process of cleavage, the original character of which has been so altered that it is impossible to determine the relation of the primary mesoblasts to the micromeres and macromeres of the typical unequal cleavage. Fortunately, however, Vejdovsky has succeeded in following their mode of origin

in *Rhynchelmis*, where they arise in a manner closely similar to that studied by Whitman in *Clepsine* (Nos. 45, 48).

After the formation of the first pair of secondary mesoblastic cells others are formed by successive divisions of the primary mesoblasts, which in the meantime gradually sink below the surface of the blastula and are finally quite included in the cleavage cavity (Figs. 24-30). Thus arise two parallel rows of mesoblastic cells which lie in the cavity of the still spherical blastula and define the antero-posterior axis of the embryo. Posteriorly the two rows terminate in the primary mesoblasts; anteriorly they join one another in the middle line. The blastula retains its spherical form until five or six pair of secondary mesoblastic cells have become formed and the primary mesoblasts have become entirely enclosed.

This period is marked by the appearance of a large pore ("cleavage-pore") opening from the blastocœl to the outside at the lower or entoblastic pole—a remarkable phenomenon already observed by Kleinenberg. This pore is formed by the separation of the larger cells during the active periods of division, now very marked, which alternate with equally marked quiescent stages. I have never found a trace of the pore during the quiescent periods, but it is certainly present in more than one of the active periods. (Compare Figs. 22 and 26.) It seems probable therefore that it appears in several successive active periods, closing in the succeeding quiescent periods. The only explanation of it that occurs to me is that it may serve as a channel for the expulsion or entrance of liquid during the active stage, so as to avoid undue pressure on the cells during their change of form.

#### IV. GASTRULATION.

A modified embolic invagination takes place in the course usually of the third day, though the rate of development varies so greatly with the temperature and differs so widely among individuals that no general statement of the time has any value. The spherical blastula becomes flattened and slightly elongated (Figs. 31, 32), finally assuming the form of an oval plate with rounded edges (Figs. 33, 34, 39, 40). During this general change of form the cells undergo striking alterations. The larger cells of the lower pole become clearer, assume a columnar



form, and arrange themselves in a perfectly flat plate, their nuclei remaining near the peripheral ends. The smaller cells of the upper pole become greatly flattened and spread out, so as to form a pavement epithelium covering the plate of larger cells above and on the sides. The primary mesoblasts lie side by side near one end, closely surrounded by the outer cells, and from each a somewhat irregular row of cells extends downwards and forwards. The cleavage cavity is much reduced, but does not disappear until a little later.

The embryo is now bilaterally symmetrical, with well-defined dorso-ventral and posterior axes, and, except for the precocious development of the mesoblast, is closely similar to the "Plakula" of Bütschli. The germ-layers are perfectly differentiated, the entoblast occupying the entire ventral surface, the ectoblast covering the sides and dorsal surface, while the mesoblast is arranged in two diverging rows that lie near the sides of the embryo and meet each other in the median line behind. Series of sections through such embryos (see Figs. 45, 46), as well as optical sections of entire embryos (Figs. 35, 42), show in the clearest manner that the mesoblastic rows end abruptly in front at the sides, without extending across the median line. At a much later period they grow forward and join above the mouth, this forward growth being effected in the main by an actual migration of the cells, and in no case by proliferation from either ectoblast or entoblast.

The embryo now becomes concave on its lower side, so as to form a large blastopore occupying the entire ventral aspect (Fig. 35). By the folding in of its sides this blastopore then assumes the form of a longitudinal slit (Fig. 37), and rapidly closes from behind forward, the anterior part remaining open as the mouth (Figs. 36, 42). During these changes the anterior lip of the blastopore undergoes no change; the general history of the blastopore is, therefore, closely similar to that *Eupomatus*, as described by Hatschek (No. 23). The anus is not formed until the end of larval life.<sup>1</sup>

<sup>1</sup> There is a considerable variation in the closure of the blastopore, owing to differences in the rate of folding between the sides and the posterior margin of the blastopore. As a rule the sides fold in more rapidly than the hinder lip, thus giving rise to a slit-like blastopore, but in some cases the reverse is true, so that the blastopore never appears as a slit, but always as a rounded opening.

## V. GENERAL HISTORY OF THE GERM-BANDS.

I shall use the term germ-band to mean the composite structure extending along either side of the body from the primary mesoblast to the dorsal side of the mouth, and consisting in its middle portion of the three strata of cells referred to at p. 389.

1. *The Mesoblast.* — In its earliest form, as it occurs in the blastula, each germ-band consists only of the primary mesoblast with the corresponding row of mesoblastic cells extending forwards from it and joining its fellow in front (Figs. 30, 31, 32). As the blastula flattens shortly before the invagination, the mesoblastic rows are carried out towards the sides of the embryo and their anterior ends become widely separated. As the invagination proceeds the mesoblastic rows undergo a two-fold change. First, they grow forward and upwards, as already described, so as to approach one another above the anterior lip of the blastopore (Fig. 43); and second, their middle portions are carried still further downwards so as to lie on the ventral side, though they are still widely separated. Meanwhile the ectoblast becomes thickened immediately over the mesoblastic cells and thus forms the outer or ectoblastic stratum of the band. This thickened area of the ectoblast everywhere accompanies the underlying mesoblastic band, but is somewhat wider. Dorsally and ventrally it passes rather suddenly into the large-celled, flattened epithelium that forms the upper and lower investment of the embryo (Fig. 41). Sections at this stage show the ectoblast to be still everywhere composed of a single layer of cells. In front the thickened ectoblastic areas fade away into the pavement epithelium of the dorsal surface (surface views in Figs. 33, 35, 36, 41, 43; sections in Figs. 52, 53, 67, 68; see explanation of plates).

It is necessary to refer at this point to the group of enlarged ectoblastic cells known as "Schluckzellen," which appear at an early stage at the anterior part of the body in the embryos of some Hirudinea, and in a number of the Oligochæta, including some species of *Lumbricus*. These cells, whose mode of origin has been carefully studied by Hatschek in *Criodrilus* (No. 18), and by Vejdovsky in a number of Oligochæta (No. 46) have been shown by the last-named author to be larval excretory organs. They are at first enlarged ectoblast cells which lie at the

surface and form the dorsal lip of the blastopore; at a later period they are overgrown by the ectoblast and thus come to lie between the ectoblast and entoblast in the median dorsal line. This account of their position and mode of origin holds true for *Lumbricus communis* and *Lumbricus terrestris*, but in *Lumbricus fetidus*, the form which I have most carefully studied, they appear to be wholly wanting (see p. 422). In this species the dorsal lip of the blastopore is formed by large entoblast cells covered dorsally by flattened cells of the ectoblast (Figs. 35, 46).

As development proceeds the lateral areas of thickened ectoblast extend forwards until they meet above the blastopore, the "Schluckzellen" (in *L. communis* and *L. terrestris*) being thus covered and pushed somewhat backward. At a slightly later period these ectoblastic bands extend ventrally around the blastopore until they meet and quite enclose it on the ventral side (Fig. 43). The thickened ectoblastic lips thus formed now grow into the blastopore to form the stomodæum which is in this manner fully established very soon after the narrowing of the blastopore. The opening into the archenteron appears never to close, and even before the establishment of the stomodæum the embryo begins to swallow the albumen in which it floats.

The middle stratum of the germ-bands can first be distinguished while the embryo is still nearly spherical, immediately after the establishment of the stomodæum. At this period close examination of the surface of the bands near their middle part shows some of the ectoblast cells to be arranged in distinct longitudinal rows, each one of which terminates posteriorly in a larger cell or teloblast (Figs. 47, 49; and Plate XIX.). Sections at this stage show that the cells of these rows, and the teloblasts at their extremities, form a part of the general ectoblast, though here and there they are overlapped by the adjoining cells, and in some cases may be actually covered (Figs. 53, 54, 66-68). In later stages the teloblasts and corresponding cell-rows gradually sink below the surface and thus give rise to a stratum of cells lying between the mesoblast and the outer ectoblast, but imbedded in, and clearly forming a part of, the latter (Figs. 70, 71, 72). Their precise mode of origin and ultimate fate are described further on.

The germ-bands are now fully established, and their subsequent general development may be briefly sketched as follows:

The embryo rapidly elongates, becoming successively ovoid, elongate, and finally vermiform. Upon the full establishment of the germ-bands the teloblasts and cell-rows have a definite and characteristic arrangement which is retained throughout the development. This arrangement (Figs. 47, 48, 49, 63) is essentially the same in the three species of *Lumbricus* I have examined, and an exactly similar arrangement exists in the embryos of a small fresh-water Oligochaete which I have unfortunately not been able to determine, but which is almost certainly not *Lumbricus*. The primary mesoblasts lie behind and somewhat above a horizontal plane passing through the middle of the body (Fig. 38), in contact with each other in the median line. New cells are always formed at the postero-lateral angles of these teloblasts (Fig. 60), and the mesoblastic rows curve thence forwards and downwards around the teloblasts, nearly or quite meet in the middle ventral line, and then pass outwards and forwards, soon widening into a pair of flattened plates in which the coelomic cavities are developed long before their concrescence on the ventral side (Figs. 63, 69). The neuroblasts are much further forwards than the mesoblasts, and lie just opposite the lower (mediad) edge of the mesoblastic plate. The two nephroblasts lie side by side somewhat further back and a little towards the dorsal side. The lateral teloblast, which I have found in early stages of *L. communis* only, lies just in front of the nephroblasts opposite the upper edge of the mesoblastic plate (Figs. 61, 67).

The growth of the germ-bands keeps pace with that of the embryo generally. The teloblasts are carried steadily backward, each leaving behind it a trail of cells derived partly by continual divisions of the teloblast, partly by subsequent divisions of the cells thus formed. After the most careful study of a large number of germ-bands in surface view, and in transverse and longitudinal sections, I can state positively that the several cell-rows — mesoblastic, neural, nephric, and lateral — are wholly derived from the corresponding teloblasts, and in no other way. I have repeatedly observed all stages of division in all of the teloblasts, in the cells derived from them, and in the outer ectoblast. The division-figures prove beyond question that the cell-rows elongate in the manner described, and I have never seen the least indication of any other mode of increase.



In early stages all the cell-rows are but one cell in width at their hinder ends. Passing forwards they soon become several cells wide and deep, and the two nephric rows on each side fuse completely. Only the neural and the mesoblastic rows can be traced around the mouth; the others fade away at the sides of the stomodæum. As the embryo enters the later stages of development the teloblasts break up into smaller cells, so that each cell-row, now several cells in width throughout its whole length, terminates behind in a group of undifferentiated cells (Figs. 63, 97). The neuroblasts, nephroblasts and lateral teloblasts first disappear; the primary mesoblasts persist to a much later period, and only disappear near the time of hatching, when the proctodæum is formed.

Concrescence of the bands begins in front and proceeds thence regularly backwards, the union of the bands taking place first in the median ventral line, afterwards in the median dorsal line, as the mesoblastic bands extend around the archenteron. It begins at a very early period, as already described, with the anterior fusion of the ectoblastic part of the bands to form the stomodæum. The mesoblastic bands move together at a much later period. As the bands come together the neural rows of the two sides come into contact in the middle line, fuse more or less completely together, and thus give rise to the ventral nerve-chain. Posteriorly the bands diverge up to a very late stage of development, having the disposition shown in Fig. 63. Owing to this divergence and the subsequent junction of the bands at the extreme posterior end, a somewhat elongated space is enclosed by the hinder part of the bands, in which the ectoblast and entoblast are directly in contact.

From the foregoing account it will be seen that the cephalic lobe (prostomium, or head) arises by concrescence of the anterior extremities of the same germ-bands that form the trunk.

A more detailed account of the formation of the head is given at page 407.

## VI. GENERAL HISTORY OF THE MESOBLAST.

1. *General Differentiation.* — The forward growth and union of the mesoblastic bands to form the cephalic mesoblast has already been described. Upon the completion of this process the meso-

blastic bands form a complete ring which encircles the archenteron longitudinally with its middle part drawn somewhat towards the ventral aspect. Posteriorly the bands are a single cell in width; anteriorly they soon widen into flat plates which are widest in the middle region, narrowing somewhat as they pass upwards at the sides of the stomodæum. It should be borne in mind that the cephalic mesoblast (which forms the anterior median portion of this ring) is formed mainly by an actual migration of cells from the anterior ends of the mesoblastic bands. At a somewhat later period some of the cells situated at the edges of the mesoblastic bands lose their connection with the others, pass upwards between the ectoblast and entoblast, and thus give rise to what I have called at page 389 the *migratory mesoblast*; the remaining portion of the mesoblastic bands (in which the coelomic cavities afterwards appear) constituting the "trunk-mesoblast." Anteriorly the migratory mesoblast of the trunk-region is continuous with the cephalic mesoblast (Fig. 50); toward the ventral side it passes suddenly into the mesoblast of the germ-bands.

The cells of the migratory mesoblast do not form a continuous layer, but remain scattered, become branched, and form a beautiful network (Fig. 89) that encloses the entire archenteron. In this network at least two kinds of cells can be distinguished. The first are enormously long branching muscle-fibres arranged in a longitudinal and a circular set which cross at right angles and form an open network. The substance of the fibres stains deeply with hæmatoxylin and is nearly homogeneous; the nucleus is situated near the middle of the fibre, attached to its side, and surrounded by a small quantity of granular protoplasm. The fibres are sometimes simple, but more usually subdivide towards their extremities into excessively fine twigs, and occasionally a cluster of branches is given off near the middle of the fibre at right angles to its general course. The granular protoplasm surrounding the nucleus in some cases also gives off branches, but these are easily distinguishable from the muscular branches.

Cells of the second kind are much less numerous than the others. They are granular branching cells having the general appearance of large connective-tissue cells. In some cases their branches appear to join those of other similar cells and the pro-

toplasmic branches of the muscle-cells, but I have not fully satisfied myself on this point. I have searched in vain for nerve-cells in this network.

The migratory mesoblast of the trunk-region is gradually displaced by the trunk-mesoblast of the germ-bands, which as development proceeds, steadily extends both dorsally and ventrally, forcing its way between the ectoblast and entoblast as it grows. The two bands finally meet and fuse with one another, first along the median ventral line from before backwards, subsequently along the median dorsal line in a similar manner. From it (*v. infra*) are developed the permanent muscles of the trunk, which are differentiated from the mesothelial walls of the cœlomic cavities and are unbranched (as may be clearly seen in preparations macerated in Hertwig's fluid). The longitudinal fibres are the first to appear, forming on each side a longitudinal bundle that lies just opposite the boundary between the nephric and neural cords (Figs. 72, 90, 91). A second bundle appears later just outside the nephric cord. I have been unable to determine whether the larval branching muscle-fibres disappear or remain embedded in the adult body-wall.

In the head-region the mesoblastic cells become amœboid and branched and ultimately arrange themselves so as to enclose a single median cavity (prostomial or head-cavity) traversed by branching contractile cells.

From the foregoing account it appears that the trunk-mesoblast is a "mesothelium," the migratory mesoblast of the trunk a typical "mesenchyme," while the cephalic mesoblast is of an intermediate character. All these cells have, however, a common origin, and the distinction between "mesothelium" and "mesenchyme" in the embryo as originally made by the Hertwigs (No. 25) is here of wholly secondary importance (as has been shown to be the case in other annelids by Kleinenberg and Hatschek). The migratory mesoblast of the trunk appears to be a special larval musculature precociously developed in order to enable the embryo to manage the enormous mass of albumen with which its body is distended.

2. *Origin of the Cœlom.*—The trunk-cavities appear in the mesoblastic bands in regular succession from before backwards (Figs. 50, 63, 97). In longitudinal sections the bands are seen to be posteriorly but one cell in thickness; further forward

they are arranged in two layers which still further forward are seen to be the somatic and splanchnic layers, the coelom appearing between them. Posteriorly the cells of these layers have a pyramidal form and dove-tail together with great regularity. Further forward, as they separate, the narrow inner overlapping ends of the cells remain in contact, the coelomic cavities appearing as spaces between them, so that each cell forms part of a dissepiment. The number of cells rapidly increases, however, as the coelomic cavities enlarge, so that the dissepiments, which are at first in contact above and below, are separated by the somatic and splanchnic epithelium, and also become two-layered.

The cavities of the two bands are at first wholly separate, since they make their appearance some distance behind the point of conrescence, as shown in Fig. 69. As the bands grow together the corresponding cavities of the two sides are opposed to one another and finally fuse, at first incompletely on the ventral side where a ventral mesentery persists, afterwards completely on the dorsal side, so as completely to surround the archenteron.

The most anterior pair of cavities (see Fig. 50) lie at the sides of the stomodæum, bounded in front by a mesoblastic wall which at first is horizontal, but subsequently becomes oblique and finally vertical. These cavities give rise to the coelom of the first post-oral somite, in which nephridia never develop. The following pair of cavities give rise to the second somite, which has no nephridia of its own, but receives the funnels of the following or third somite. The first pair of setigerous glands are developed in the second somite.

The head-cavity appears in the middle line above the stomodæum at about the same period as the anterior pair of trunk-cavities, directly between which it at first lies. Series of sections in all planes show most clearly the unpaired character of the head-cavity from its first appearance onward. Its walls are bounded by a distinct layer of mesoblastic cells, and its cavity is traversed by a loose network of branching contractile cells. On the dorsal side these cells are continuous posteriorly with the migratory mesoblast of the trunk, and the head-cavity itself appears to be continuous with the lacunæ between these cells. In later stages, however, as the trunk-mesoblast extends around the dorsal side of the archenteron, the head-cavity acquires a definite hinder limit, formed by the dorsal union of the first pair



of dissepiments (Fig. 80). Into this cavity projects the foundation of the cerebral ganglia, which is covered inwardly by a layer of mesoblast.

In passing from above downward in a series of horizontal sections the prostomial cavity first appears (Figs. 55 and 56), and then a little further down the anterior pair of coelomic cavities come into view at the sides of the stomodæum. In slightly later stages all three cavities may be seen in one section, as shown in Fig. 58. I find it difficult to understand Kleinenberg's account of the matter, and am forced to conclude that the two lateral cavities by the fusion of which he supposed the prostomial cavity to arise, are simply the anterior pair of trunk-cavities, and that he overlooked the partition separating them from the median cavity. Their true relations will be made clear by comparison of Figs. 50, 57, and 58.

3. *Blood-Vessels*.—The first blood-vessel to appear is the ventral or sub-intestinal. It makes its appearance in the median ventral line, shortly after the fusion of the mesoblastic plates in this region, as a space lying between the wall of the archenteron and the mesoblast (Fig. 72). At first it has no proper wall, being bounded below by the mesoblast and above by the entoblast, so that it would seem to represent a part of the original cleavage cavity. Here and there along its course, however, a single cell can be seen on its dorsal side applied to the entoblast. In later stages—or what amounts to the same thing, further forwards—these cells increase in number, so that the vessel becomes enclosed in a distinct wall of its own and appears to lie in the splanchnic mesoblast as figured in Fig. 25 *a*, Pl. XI. of Kleinenberg's paper. The most careful examination has failed to satisfy me as to the precise origin of the walls of this vessel. But without being able to give absolute proof, I believe them to arise from cells which migrate out of the mesoblast. In any case the cavity of the vessel would seem to be of the same character as the lacunar cavities between the cells of the migratory mesoblast, which are for a time at least in connection with the head-cavity.

As to the development of the dorsal vessel, I can do little more than confirm Kowalevsky's interesting discovery (afterwards extended by Vejdovsky to *Criodrilus*, No. 43) of its double origin. Shortly after the appearance of the ventral vessel two

lateral vessels make their appearance near the outer or dorsal edge of the mesoblastic plate (Fig. 72). They develop in precisely the same way as the ventral vessel, first appearing as spaces between the splanchnic mesoblast and the archenteric wall, but ultimately acquiring walls of their own.

In the posterior region these vessels lie parallel to the ventral vessel, quite on the ventral side of the embryo. On tracing them forwards they are found to assume a lateral position, and finally to pass towards the dorsal side, where they finally unite in a single vessel which runs forwards in the median line (Fig. 51).

The arrangement of the longitudinal trunks at this period is almost precisely like that of many adult tubicolous Polychæta (*Amphitrite*, *Melinna*, *Lanice*; see Meyer, No. 35, Taf. 23); and Beddard (No. 4) has shown that the dorsal vessel remains more or less completely separated into two parallel trunks in a number of Oligochæta (*Megascolex*, *Microchæta*, *Acanthodrilus*). Beddard is inclined to consider this the primitive mode of development—a view which, however, seems at present to rest on insufficient evidence.

The dorsal vessel is formed by the progressive backward concrescence of the two lateral vessels—a process which on the whole keeps pace with that of the mesoblastic bands and is only finally completed near the time of hatching. The vessels lag somewhat behind the remaining mesoblast, however, so that in the posterior region they still lie at the sides when the mesoblast has entirely surrounded the archenteron, as in Fig. 72, Pl. XX. The cells of the mesoblast lying above the lateral vessels seem to pass upward in large part by migration, and only become arranged in definite somatic and splanchnic layers at a later period.

The first of the circular vessels to appear are the circum-œsophageal vessels or pseudo-hearts, which are developed in the splanchnic mesoblast in connection with the unpaired anterior part of the dorsal vessel, and as far as I have been able to observe are surrounded with definite walls, from the start. The circular intestinal vessels develop considerably later, and I have never been able to distinguish them until after the complete fusion of the lateral longitudinal trunks to form the median dorsal vessel.

## VII. THE ENTOBLAST.

Just before the invagination of the gastrula the entoblast forms a flat plate of prismatic cells covered dorsally by the mesoblast and the thinned ectoblast, and at the sides by the mesoblastic bands and the thickened areas of the ectoblast. The nuclei lie near the lower ends of the cells (Figs. 34, 45). During the invagination the anterior edge of the entoblastic plate remains stationary, while the lateral margins bend downwards and the posterior margin grows forward. The superjacent ectoblast takes part in this change, but the thickened areas overlying the mesoblastic bands are left behind, so that the archenteron is covered below with very thin large polygonal cells (Figs. 36, 41, 42). At the completion of the invagination the archenteron has a nearly spherical form (Fig. 38). Its cells are clear, columnar, with their nuclei near the inner ends. As soon as the embryo begins to swallow the albumen, which is done almost immediately after the narrowing of the blastopore, the whole body becomes greatly distended and enlarged, so that the archenteric wall becomes much thinner and the cells undergo a marked alteration in form. Their cell substance also changes in character, the protoplasm now containing numerous slightly staining globules of various sizes. I am unable to explain by what process absorption takes place; the appearances indicate that the albumen is taken bodily into the cells, *amœba*-fashion.

The ingrowth of the stomodæum and the concomitant increase of the mesoblast in the anterior region cause still further changes in the form of the archenteron. The stomodæum grows backwards and downwards in the median line (see p. 25), pushing the archenteric wall before it, while the pressure within the archenteron causes it to bulge forward into the head-cavity, which is thus often almost or quite obliterated. In early stages this forward bulging is often so extreme as to cause the mouth to face directly downwards.

The later changes may be very briefly treated. The archenteron continually elongates with the growth of the body, its hinder extremity remaining in contact with the ectoblast just behind the primary mesoblasts, at which point the stomodæum is afterwards formed; in front the archenteron becomes widely separated from the extremity of the body, owing to the elongation

of the stomodæum and the growth of the anterior somites (Fig. 50).

The ingrowing stomodæum (see following section) pushes the archenteron backwards as far as the sixth somite, which is its extreme limit in the adult and marks the point of union of the pharynx and the œsophagus. Thus the œsophagus is lined by entoblast, as are also the calciferous glands which develop as diverticula from it. At the time of hatching the various regions of the alimentary canal are completely differentiated, and the typhlosole is established as a deep infolding of the dorsal median wall of the intestine. I have not yet attempted to follow in detail the histological differentiation of the alimentary wall.

#### VIII. THE ECTOBLAST AND ITS PRODUCTS.

I. The origin of the general ectoblast of the ectoblastic stratum of the germ-bands and of the stomodæum have already been described. At the end of the gastrulation the ventral aspect of the embryo is covered by a large-celled pavement epithelium which passes abruptly at the sides into the swollen superficial granular cells of the germ-bands. A little later some of the cells along the median ventral line become enlarged and covered with short cilia which cause the embryo to rotate slowly in the longitudinal vertical plane. The ciliated cells are at first arranged in a single irregular series along the median line, and the individual cells are separated from one another by groups of smaller non-ciliated cells. At a later period the ciliated cells come into contact and form an irregular continuous double row which form the floor of a slight but distinct ventral groove. In front this groove nearly disappears, but the ciliated cells are continuous with the ventral lip of the stomodæum, and the cilia extend around the lips of the stomodæum into its cavity. In still later stages the ciliated cells gradually disappear, apparently by breaking up into ordinary ectoblastic cells and losing their cilia. I am certain that they take no part in the formation of the ventral nerve-chain, which is entirely formed by concrescence of the two neural rows. As the germ-bands spread around the body, the pavement-epithelium of the dorsal and ventral surfaces is gradually converted into a columnar epithelium which persists as the hypodermis and is covered by the cuticle.



2. *Stomodæum*. — The foundation of the stomodæum by concrescence of the ectoblastic layer of the germ-bands has already been described; its late development is shown in Figs. 79–82. As the stomodæum grows in, its cells become ciliated, considerably enlarged, and their substance becomes extensively vacuolated. Somewhat later the walls of the stomodæum become several cells deep, consisting of a deeper stratum of small granular cells and an irregular superficial stratum of clear ciliated vacuolated cells, which are often dovetailed in with the smaller cells, but sometimes lie flat on their outer ends. Still later the larger cells disappear completely, and the stomodæum consists only of columnar, granular cells derived from the smaller deeper cells.

The stomodæum grows inwards exactly between the mesoblastic cavities of the first somite (which lie at its sides), and ventral to the head-cavity. It grows thence backwards as far as the dissepiment between the fifth and sixth somites, where its limit can be distinctly made out in vermiform embryos 15 mm. long and nearly ready to hatch. In such embryos the circum-oesophageal vessels are fully established, so as to show clearly the limit between the pharyngeal and oesophageal regions. The first aortic arch, which is smaller than the following ones, is found in the sixth somite, immediately behind the limit of the stomodæum. It is clear therefore that the stomodæum gives rise only to the pharynx, and that the oesophagus, with its calciferous glands, is derived from the archenteron, — a result in accordance with Vejdovsky's account of the stomodæum in *Rhynchelmis* (No. 44, p. 100). In front of the sixth somite the dissepiments break up more or less completely to form a mass of radiating fibrous structures which suspend the pharynx in a large irregular cavity which extends forward about to the second somite. Still further forward the cœlom is wholly obliterated, being filled, like the prostomial cavity, with a spongy mass of muscles, connective tissue, vessels, and nerves.

I may at this point conveniently speak of the change of position which the cephalic ganglia undergo during the differentiation of the stomodæum. When first formed, these ganglia lie, as we have seen, at the extreme anterior part of the body in the prostomial cavity. But as the stomodæum grows inwards the ganglia travel gradually backwards until they come to lie in the third somite in the anterior extremity of the cœlom. From

them the œsophageal commissures pass nearly vertically downwards to the sub-œsophageal ganglion, which likewise lies in the third somite<sup>1</sup> (see p. 417).

The stomodæum of *L. fetidus* differs remarkably from that of the other species studied. In *L. terrestris* and *L. communis* the invaginated ectoblast is but slightly thickened and is directly continuous with the general ectoblast. In *L. fetidus*, on the other hand, the ventral lip of the stomodæum becomes expanded like a funnel, and greatly thickened, especially towards the sides, so as to form a swollen mass of elongated fusiform cells which in sagittal sections (Fig. 82) is strikingly like a taste-bud. This mass (which seems to correspond to the "Mundwulst" of *Criodrilus*) is transversely elongated so as to form the entire ventral lip of the stomodæum. In some cases it is slightly bilobed, but usually is nearly uniform in thickness. The cells are attenuated towards their outer ends, and the peripheral ones are curved so as to bring the ends of all the cells together at the surface. Ventrally the cells of the stomodæal lip abut against those of the ventral ectoblast, from which they are separated by a very distinct line of demarcation. Inwardly they are also separated, though less markedly, from the cells of the narrow part of the stomodæum. The cells of the thickened lip are slightly granular, but not more so than those of the inner part of the stomodæum; their nuclei are large and conspicuous. In later stages the thickening gradually disappears and its cells appear to be converted into ordinary columnar epithelial cells like those forming the general wall of the stomodæum.

I am unable to say whether this larval structure is to be regarded as a glandular or a sensory apparatus. It suggests in its structure, position and mode of origin the paired larval sense-bulbs, or primary sense-organs of the lip found in the Hirudinea (see Whitman, No. 52, p. 159), which by fusion in the middle line would give rise to precisely such a thickened lip. Moreover, Hatschek figures (No. 18) the "Mundwulst" of *Criodrilus* as arising from completely separate foundations. On the other hand, it is difficult to understand the use of so highly developed a sense-organ in but one species of *Lumbricus*, and its presence is so obviously correlated with the peculiar character of the albumen in *L. fetidus*, that I am inclined to regard it as a larval digestive gland. It will be remembered that in this species the albumen is tough and jelly-like, differing markedly from the slimy, mucus-like albumen of other forms. It seems therefore not unlikely that the cells of the organ in question may pour forth a secretion to soften the albumen and thus facilitate its ingestion by the young embryo.

In *L. communis* and *terrestris* there is no indication of this structure at any period. In both these species, however, peculiar deeply staining gland-like cells are found in the anterior part of the stomodæum (see Fig. 81), lying for the most part in its ventral wall, but also extending up on the sides, in some cases reaching the dorsal wall. These cells may perhaps be of the same na-

<sup>1</sup> This backward shifting of the cephalic ganglia is characteristic of many Oligochaeta. See Vejdvsky, No. 44.

ture as the "larval gland-cells" of *Clepsine* (Whitman, No. 52, p. 157), though they are not pigmented and have a somewhat different position.

The later differentiation of the pharynx is effected by an enormous thickening of its mesoblastic investment on the dorsal side, the ventral mesoblast remaining extremely thin.

3. *Proctodæum*. — The proctodæum is very long delayed in development, only making its appearance near the end of foetal life, when the body has an elongated form and concrescence of the germ-bands is nearly complete. It is formed as a hollow invagination of ectoblast which pushes its way between the hinder ends of the mesoblastic bands, and soon fuses with the archenteric wall. I have not been able certainly to determine the important question of its precise morphological relation to the ends of the germ-bands, owing to the fact that before its formation the primary mesoblasts break up into smaller cells and thus render the hinder limits of the bands somewhat difficult to determine. In *Polygordius*, and many other annelids, the proctodæum is formed behind, or dorsal to the primary mesoblasts, *i.e.* outside the mesoblastic ring formed by the germ-bands; and this seems to be the typical position of the anus in annelids generally. In *Lumbricus* towards the end of foetal life the primary mesoblasts break up into a group of cells from which the mesoblastic bands (now entirely united along the ventral line) extend forward (Fig. 97). As the proctodæum grows inwards this mass of cells grows upwards at the sides of the proctodæum in two horns, which finally unite in the dorsal line above it (*cf.* Figs. 95–97). Thus the mesoblastic ring ultimately comes to surround the proctodæum behind, as it does at a much earlier period the stomodæum in front, the middle portion of the ring having meanwhile undergone concrescence throughout its whole extent. The stomodæal invagination has the form of a longitudinal slit which at first faces upwards owing to the curvature of the body, but gradually is turned backwards as the body straightens out. Its walls fuse completely with those of the archenteron and assume the same histological character, and every trace of the limit between them disappears. It is therefore impossible to determine how far forward the proctodæum extends, but its extent is certainly very limited.

## IX. NERVOUS SYSTEM.

Apart from the discovery of the neuroblasts my results on the origin of the nervous system differ materially from those of Kleinenberg, and have, as I believe, an important bearing on the question as to the relation between the head and the trunk. Two principal questions are involved, namely: (1) do the cerebral ganglia arise independently of the ventral chain, and (2) do they arise from a median unpaired apical plate (Scheitelplatte)? As far as *Lumbricus* is concerned both these questions must be answered in the negative. My preparations show clearly, I think, that the entire nervous system has a double (bilateral) origin and is formed by a process of concrescence; and furthermore, that the foundation of the cerebral ganglion of each side is simply the thickened anterior extremity of the corresponding neural row.

In its first recognizable condition the nervous system is represented (Fig. 47) by a short neural row lying *at the surface of the germ-band* on each side the body. Each row terminates behind in a neuroblast; anteriorly it passes up at the side of the mouth and is apparently lost in the general ectoblast. Its structure in front can only be made out by the study of oblique longitudinal sections passing in such a plane as to cut the neural row lengthwise (*i.e.*, a longitudinal plane inclined about 45 degrees to the sagittal plane). After many unsuccessful attempts I succeeded in securing such a series, consisting of 27 consecutive sections through an embryo slightly older than that shown in Fig. 47. This series shows the relations so clearly and is of such importance that I figure six of the sections (Plate XX., Figs. 73-78).

Figure 73 is the uppermost, *i.e.*, the one nearest the surface. It passes lengthwise through the posterior part of the germ-bands, cutting the primary mesoblast at *M*, the right neuroblast at *Nb*, and showing the connections of these teloblasts with the corresponding rows. The succeeding sections pass at successive lower levels, and, owing to the curvature of the germ-bands, show the forward continuation of the bands. Figure 74 is the section adjoining Fig. 73; it shows the neural row *nc* passing forwards and upwards at the surface of the body. Figure 75, two sections further on, is of great importance. It shows that the neural



rows (which here represent the future œsophageal commissures) are partly covered in at the sides by the general ectoblast, and that their extreme anterior ends are enlarged and partially united with the dorsal ectoblast to form the foundation of the cephalic ganglia. This section shows also the beginning of the migration of the anterior mesoblast cells to form the cephalic mesoblast. Figure 76 is a more enlarged view of part of the adjoining section to show the continuity of the neural row with the cephalic foundation. Figure 77 is four sections further along, and shows the complete disappearance of the neural rows towards the median line. Figure 78, four sections further on, passes in front through the median line, and shows the mouth-cavity, the group of "Schluckzellen" which forms the anterior limit of the mouth and were visible already in Fig. 77, and the large ciliated cells of the median ventral surface. In sections at a still lower level (*i.e.*, on the left of the median line) the neural and mesoblastic bands of the left side appear in oblique section. This clearly demonstrates the fact *that at this period, although the gastrula is fully established, the germ-bands are completely separated in front.* The series shows furthermore that there is no apical neural plate, the cephalic ganglia arising independently on either side of the median line. It shows finally the important fact, that the cephalic ganglia arise from the same neural rows that give rise to the œsophageal commissures and the ventral chain, though their development is slightly in advance of the other parts (see p. 434).

At a slightly later period the mesoblastic, neural, and ectoblastic elements of the opposite sides of the body grow together in the median dorsal line above the mouth (*cf.* Fig. 43.), and the unpaired cephalic cavity appears just between the two cephalic ganglia (Fig. 56). At this period a bridge of neural tissue, closely united with the ectoblast, can be traced across the median line from one cephalic ganglion to the other (Figs. 55, 56). I have not certainly determined whether this bridge is formed by proliferation of the overlying ectoblast or by growth of the neural structures already existing. I incline, however, to the former view, because there appears to be a complete fusion of the neural tissue with the ectoblast in the middle line.

The question whether the cephalic ganglia, like those of the ventral chain, are derived from the neuroblasts or by proliferation from the general ectoblast, still remains in doubt. This

question, however, appears to be largely one of terms only, for both the neuroblasts and the neural cells form at this period part of the general ectoblast (Figs. 53, 73), and all the cells are constantly undergoing division. The fact that the neuroblasts, when first distinguishable, lie some distance behind the mouth, seems to indicate, however, that the cephalic ganglia and the œsophageal commissures are first differentiated *in situ* directly out of the ectoblast, and that the neuroblasts are afterwards differentiated as special centres of apical growth as the embryo begins to elongate.

Soon after their union the cephalic ganglia project into the prostomial cavity, and become surrounded by a mesoblastic investment. As the stomodæum grows inward, these ganglia, as well as the commissures extending around the œsophagus, are carried backwards until they lie in the third somite, which is their permanent position (*cf.* Figs. 50, 51, 79, 81).

The ventral chain arises entirely by concrescence of the two neural cell-rows, a process which has been accurately described by Kleinenberg. I have sought in vain for any indication of the participation of a median element ("Mittelstrang") in the formation of the nerve-cord. The lateral nerves are formed as outgrowths from the ganglionic cord.

Concrescence of the neural rows begins in the first somite immediately behind the lower lip, where a slight ganglionic swelling is formed. A second more distinct double swelling is found in the second somite, a third in the third somite, and so on through the body. As the cerebral ganglia travel backwards in the manner described above, the ganglia of the first three somites fuse completely together to form the ganglionic mass known as the subœsophageal ganglion, which would therefore seem to represent three pairs of ganglia. It is, however, possible that the original anterior enlargement in the first somite is not morphologically to be regarded as a ganglion.

A careful study of cross-sections of the neural cords along the region of concrescence brings out the fact that the ganglionic regions are the first to unite, and that they can be distinguished as enlargements of the neural cords before concrescence begins; *i.e.* behind the point of union. Figures 90 and 91, Pl. XXII., illustrate this point. The former, which is taken through the region of the commissures, shows the neural cords perfectly

separate. The latter, two sections further back, passes through a ganglionic region and shows the enlarged cords joined by a narrow transverse bridge of neural tissue. This alternate separation and junction of the neural cords can be traced for a considerable distance behind and in front of the sections figured. All my preparations indicate that the transverse bridge of tissue uniting the ganglia is a product of the neural cords and has no connection with the superficial ectoblast.

I can add little to Kleinenberg's account of the histological differentiation of the ventral cord. The fibrillar substance appears some time after concrescence of the neural cords, appearing in cross-sections of the ganglionic regions as a clear punctate, bilobed mass on the dorsal side just beneath the mesoblastic sheath, which is still very thin. On tracing the sections forwards the bilobed fibrillar mass grows steadily larger, and may be seen to be separated into two distinct bundles in the commissural regions, the interval between the two bundles being occupied by a triangular mass of cells that extends upward from the nerve-cells on the ventral side and comes into contact above with the dorsal mesoblastic investment.

The neurochord first distinctly appears in the ganglionic regions in the upper part of the fibrillar mass, and in its earliest distinguishable condition already shows the three fibres characteristic of the adult. Its precise origin is difficult to determine. In the ganglionic region it unquestionably lies in the fibrillar mass, and may often be seen to be separated by a distinct line from the mesoblastic investment. In the commissural region it becomes lost in the apex of the mass of cells that separates the two halves of the fibrillar mass. All my preparations indicate that the giant-fibres arise by direct differentiation from the dorsal portion of the fibrillar mass, and not from the mesoblastic investment,—a conclusion which is entirely opposed to Vejdovsky's apparently clear and careful account (No. 44, p. 93). There can be little doubt, however, from recent anatomical studies (see Nos. 17, 37, 42) of the essential correctness of the original view of Leydig and Claparède, according to which the colossal fibres of the neurochord are specially modified nerve-fibres, which have probably assumed a supporting function.

## X. EXCRETORY ORGANS.

The following account of the development of the nephridia will be facilitated by a short review of our present knowledge of the subject. For the sake of brevity I shall pass over most of the earlier literature and consider only the results of more recent studies. (For fuller reviews of the literature, see Vejdovsky, No. 44; Bergh, No. 8; Eisig, No. 16; and Meyer, No. 35.) The development of the nephridia in the Polychæta has been most carefully studied by Meyer, to whose interesting work reference will be made further on. Our present knowledge of the nephridia in the Oligochæta rests in the main upon the beautiful researches of Vejdovsky, whose great work on the Oligochæta (No. 44) must long remain a standard work of reference for students of annelid morphology.

Vejdovsky has clearly demonstrated the fact, suspected by Kleinenberg (No. 28) and definitely asserted by Bucinsky (No. 9), that the permanent nephridia in the Oligochæta arise from two sources, their inner portion being formed in the somatic mesoblast, their outer portion ("Endblase") arising as an ectoblastic invagination. According to these authors the ectoblastic portion comprises only the so-called muscular part of the nephridium, while the glandular and ciliated portions, with the peritoneal funnel, are formed from the mesoblast.

Vejdovsky has shown, moreover (No. 46), that in the course of the embryonic development of Oligochæta (*Rhynchelmis*, *Lumbricidæ*), no less than three sets of excretory organs are formed, apparently quite independently of one another. The first of these are the well-known "Schluckzellen," a short account of which has been given at p. 401. By Hatschek they were supposed to be concerned in the ingestion of albumen by the young embryo. Vejdovsky has, however, shown them to be connected with a system of delicate ciliated canals which lie in the space between the ectoblast and entoblast, and communicate with the outside through pores in the Schluckzellen; the latter structures are therefore undoubtedly to be regarded as larval organs of excretion. They wholly disappear in later stages.

The "larval excretory organs" are succeeded by independently developed "provisional" or "embryonal" organs (pro-nephridia) which are almost certainly homologous with the



"head-kidney" (Kopfniere) of *Polygordius*, *Echiurus*, and many Polychæta. These organs are in the form of a pair of straight ciliated canals situated in the anterior part of the body, above or at the sides of the alimentary canal, and extending into the head-cavity. The canals are closed internally, but open to the outside, according to Vejdovsky, at their anterior ends near the sides of the stomodæum; but according to the later studies of Bergh on *Criodrilus* (No. 8) the external opening is at the posterior end of the organ near the median line on the dorsal side of the body.

The provisional nephridia ultimately degenerate and are finally succeeded by the permanent nephridia of the trunk-region. Each of these arises (in *Rhynchelmis*) according to Vejdovsky, from a single mesoblastic cell situated on the posterior face of a dissepiment which multiplies to form a straight solid cell-cord, ending in front in a large cell from which the funnel is ultimately derived, and which soon acquires a closed lumen containing a single actively vibratile flagellum. (The flagellum does not appear in the Lumbricidæ.) This stage, which is designated as the *pronephridium*, is regarded by Vejdovsky as homodynamous with the head-kidney. The cilium-cell ("pronephrostome") of the pronephridium gives rise to the funnel of the adult, the glandular portion grows out as a loop-shaped lateral appendage from the body of the pronephridium, and the end-vesicle or muscular part is formed as an invagination from the ectoblast, which is connected with the glandular part by the persistent body of the pronephridium (No. 46, p. 683; No. 47, pp. 699, 700 for figures).

Bergh (No. 8) gives an account of the development of the nephridia in *Criodrilus*, which agrees, broadly speaking, with that of Vejdovsky, but differs in the important particular that the entire nephridium, *including the end-vesicle*, is described as arising from the somatic mesoblast.

Let us now turn to the results of Meyer in respect to the Polychæta (Nos. 35, 36), considering first his earlier studies, which were based for the most part on the study of *Polymnia nebulosa*. Meyer did not directly observe the origin of the end-vesicle (Endcanal), but gives reasons for his belief that it is invaginated from the ectoblast (*l. c.* p. 664). The most important result of his work is, however, that the funnel arises quite

separately from the glandular part of the nephridium. To quote his own words (*l.c.* p. 654): "Alle bleibenden Nephridien entstehen zu einer Zeit, wenn das Peritoneum in der bereits segmentirten Larve im Allgemeinen schon den histologischen Charakter angenommen hat, den es bei den erwachsenen Thieren besitzt. Aus faltenartigen Erhebungen desselben, welche sich gegen die gesonderte Anlage des Nephridialschlauches hin nach hinten ausstülpfen, mit den letzteren in Verbindung treten und sich mit einem inneren Wimperbesatz bekleiden, gehen die Trichter hervor; die Schläuche dagegen bilden sich aus retroperitonealen, anfangs soliden Zellstrangen, die nach ihrer Vereinigung mit den Nephrostomen einen flimmernden, terminal nach aussen durchbrechenden Achsencanal erhalten und zu zweischenkeligen Schleifen auswachsen." At page 663 he expresses the opinion that "die Nephridialschläuche einem retroperitonealen Gewebe entstammen und somit von den Peritonealtrichtern morphologisch verschieden seien," and adds that a similar mode of development is characteristic of the development of *Psymobranchus*. Meyer does not commit himself to any definite statement as to the origin of the retroperitoneal cells, but promises to discuss this question in a future work.

In his second paper (No. 36, pp. 463-476) Meyer describes in detail the development of the nephridia in *Psymobranchus*. The funnel is here shown to be derived from the anterior (mesoblastic) wall of the dissepiment (p. 472), while the glandular part arises from a single "retroperitoneal" cell which is at first wholly separate from the funnel and only secondarily comes into connection with it (p. 468). The origin of the retroperitoneal cells still remains however in doubt.

In 1886 (No. 51) Whitman announced the important discovery that the nephridia arise in *Clepsine* from a longitudinal cell-cord on each side of the body, which lies between the ectoblast and entoblast and forms part of the middle stratum of the germ-bands described by Metschnikoff many years before (No. 34). These cell-cords are derived from two large cells (nephroblasts) on each side the body, which arise from the same basis as the neuroblasts.

In 1887 I showed (No. 54) that in *Lumbricus* the nephridia likewise arise in connection with a longitudinal nephric cord that is obviously homologous with the corresponding structure

in *Clepsine*, and is likewise formed by the proliferation of a pair of teloblasts that arise directly from the ectoblast. I asserted in this paper (which was written before I had seen the works of Vejdovsky and Meyer) that the funnel arose in the peritoneal mesoblast, independently of the glandular tube which was formed as an outgrowth from the nephric cord and must therefore be of ectoblastic origin.

From the foregoing review it appears that there is still a very wide divergence of opinion in respect to the origin of the nephridia, Bergh representing one extreme (which agrees with the earlier accounts of Kowalevsky and Hatschek) according to which the entire nephridium (in *Criodrilus*) is mesoblastic; Whitman, representing the opposite extreme, asserting the origin of the entire organ from the ectoblast; while Vejdovsky and Meyer agree in asserting the double origin of the nephridia; though they differ in some very important details. I pass now to a description of my own observations on *Lumbricus*.

I have not specially studied the larval organs or "Schluckzellen," and can give no additional facts in respect to their structure and mode of origin. As stated at p. 402, I have failed to find them in *L. fœtidus*, though they are easily demonstrable in *L. communis* and in *L. terrestris*. It seems not improbable that their absence in *L. olidus* may be correlated with the presence of the peculiar glandular (?) thickening of the ventral lip of the stomodæum described at p. 413; but I have failed to find the slightest indication of any excretory function in this structure. In the other two species the remains of the "Schluckzellen" can be observed up to a comparatively late period (*e.g.* in the stages shown in Figs. 79, 80), though much diminished in size, lying as a granular mass between the entoblast and ectoblast a considerable distance behind the cephalic cavity in the median dorsal line.

As regards the "provisional" excretory organs, or head-kidneys, my observations are very unsatisfactory. They can be clearly observed in living embryos of *L. communis* at about the stage of Fig. 48 as a pair of very delicate longitudinal tubes lying apparently on the dorso-lateral wall of the archenteron, extending forward at the sides of the stomodæum and lined by actively vibratile cilia. In section (Fig. 92) they appear to be actually embedded in the wall of the archenteron, whence they

may be traced forwards into the head-cavity, and backward to a point near the dorsal median line; here they pass into the ectoblast, but I have not found any communication either with the exterior or with the head-cavity. The important problem of the relation of these organs to the permanent nephridia I have entirely failed to solve; this question can be studied to far better advantage in forms like *Criodrilus*, where the head-kidney is much larger.

We may now turn to the permanent nephridia. I have stated (p. 390) that these organs arise in connection with a continuous cell-cord of ectoblastic origin that forms part of the middle stratum of the germ-bands and lies alongside of the neural cord (Figs. 49, 59, 63, 72, etc.). Each nephric cord terminates behind in a pair of teloblasts derived from the ectoblast. The entire nephric cord is formed by the continued divisions of these "nephroblasts," which agree precisely with the neuroblasts in structure, action, and mode of origin. In early stages each nephric cord consists behind of a double row of cells, each row terminating in one of the nephroblasts. Passing forwards the rows are no longer separated by any definable limit, and the nephric cord consists of an irregular series of cells which passes upwards beside the neural row and is lost at the sides of the stomodæum; beyond this point I have never been able to trace it, either in sections or in surface-views. The general relations of the nephroblasts and the nephric cords to the remaining elements of the germ-bands are at first precisely similar to those of the neuroblasts and the neural cords, as may be seen in Figs. 53, 54, 71, 72, 90, 91. At first they lie at the surface of the body and form part of the general ectoblast; afterwards they sink beneath it so as to lie between the outer ectoblast and the mesoblast. The nephric cells closely resemble those of the general ectoblast and of the neural rows, but as a rule stain more deeply than the neural cells and less deeply than those of the ectoblast, so that all these structures appear with remarkable distinctness in cross-sections, double-stained with borax-carmin and Kleinenberg's hæmatoxylin.

In surface views of carefully stained germ-bands spread out in glycerine (Fig. 63) the nephric rudiments are clearly seen to lie along the line of the nephric cords. In both cross and longitudinal sections they may be traced directly into connection



with these cords. In the short preliminary paper already referred to I stated that the entire nephridium, excepting the funnel, was derived as an outgrowth from the nephric cord, and was therefore of ectoblastic origin—a result in accordance (except as regards the funnel) with Whitman's conclusions in respect to *Clepsine*, though this author did not follow the development far enough to determine the origin of the innermost portion of the organ. This statement was based upon the following facts, all of which have been repeatedly verified in a number of species of *Lumbricus*, and are illustrated by Figs. 83–88, Pl. XXI. The funnel arises by the division of a large cell (*f.*), which is differentiated at an early stage just at the anterior angle between the dissepiment and the somatic mesoblast (Figs. 83, 84), and manifestly arises from the mesoblast. Below and behind this cell a group of cells is formed out of which arises the body of the nephridium (*np.*). In all its stages this group of cells can be traced directly into continuity with the cells of the nephric cord. The cells are disc-shaped and are arranged in a single row which ultimately becomes perforated through its centre to form the excretory canal. Almost from the very start these cells can be clearly distinguished from an investing layer of more or less flattened mesoblastic cells which are continuous with those forming the dissepiments and ultimately give rise to the peritoneal investment of the nephridium (Figs. 83, 85, 88).

In longitudinal sections the nephric cords present posteriorly exactly the same appearance as the neural cords and are separated by a perfectly clear line from the mesoblast. Passing forward, however, this line fades away in the region of the youngest nephridia, so that it becomes extremely difficult to determine the relation of the nephric cord to the mesoblast. In this region the whole body-wall appears considerably thickened, and the only parts of the nephridia that can be positively identified, are the funnel-cells which form a regular series and are easily recognizable by their enormous nuclei. A little further forward, however, the relations can clearly be made out, and the cells are seen to be arranged in the manner already described. Whatever be its significance, there cannot be the slightest doubt that the nephridia, in their earliest recognizable form are connected in the manner described with the nephric cord,

though, owing to the fact that the nephric cords are somewhat wider than the nephridia themselves, this connection will not be seen, unless the section pass precisely through the right point, as shown for example in Fig. 86. To this fact is due, as I believe, Bergh's failure to observe the connection of the nephric rudiments with the ectoblast. I shall not undertake to explain this author's very positive statement (which is made the text of an extravagant critique of my own work), that the ectoblast is one-layered outside the nephric rudiments, until I have had an opportunity to examine for myself the development of these organs in *Criodrilus*, a subject which apparently needs re-investigation.

The appearances I have described irresistibly suggest the interpretation given in my former paper, viz.: that the funnel and the investing cells alone are mesoblastic in origin, the body of the nephridium being derived as an outgrowth from the nephric cord. This conclusion is supported by Whitman's observations on *Clepsine*, where the peculiar granulation of the nephric cells and their behavior with certain reagents renders the development of the parts even clearer than in *Lumbricus*. It fits in, moreover, completely with Meyer's observations on the Polychæta, as far as they go. The "retroperitoneal" tissue of this author (which he is careful to distinguish from the peritoneal mesoblast) corresponds exactly with the tissue from which the nephric rudiments arise, having the same relations to the investing cells and to the funnel. Unfortunately he has not yet determined its origin, and until this all-important question is answered, the nature of the glandular part of the nephridium cannot be established. It is, however, interesting to note that in *Psymnbranchus*, as in *Lumbricus*, the nephric foundations alternate regularly with those of the setigerous glands (cf. No. 36, Taf. 23, Fig. 2), apparently forming with them a continuous series, and it seems hardly too much to venture the prediction that they will be found to have a like origin.

As regards the origin of the glandular portion of the nephridium in *Lumbricus*: from the numerous preparations in my possession, I should still have no hesitation in positively reasserting my original statement as to its ectoblastic origin, were it not for Vejdovsky's careful observations on other Oligochæta, which seem to be opposed to such a conclusion. In view of

these observations I cannot deny the possibility that the glandular part *may* be differentiated from the somatic mesoblast at a very early period, fusing immediately with the cells of the nephric cord, which *may* give rise only to the end-vesicle. Until, however, the relations of the nephridia to the nephric cords (which have escaped the attention of all other observers of the *Oligochæta*) have been made clear in other forms, the question must remain open, for I do not believe it is possible to attain an absolutely certain result by the study of *Lumbricus* alone.

Whatever be the result, there can be no doubt in the case of *Lumbricus* of the intimate connection of the nephridia with ectoblastic nephric cell-cords and their partial derivation from them. The comparison of the nephric cord with the vertebrate segmental duct, which I drew in my earlier paper, has been criticised by Eisig, in an appendix to his monograph of the *Capitellidæ*, on several grounds. I may, however, point out that it differs but slightly from his own views, according to which the vertebrate segmental duct is to be regarded as the posterior extension of the ectoblastic part of an anterior nephridium, and that it gives a datum hitherto lacking to the comparison, by showing in the annelids a continuous differentiated ectoblastic structure connecting the anterior nephridia with those lying behind. As to Eisig's criticism of my comparison of the nephridia of annelids with the pronephros of Vertebrates, I fully acknowledge its force.

The nephridia rapidly elongate, and, owing to the fact that their ends are fixed, bend into a U-shape with the loop directed dorsally and laterally. Meanwhile the central cord of cells becomes perforated from end to end by a delicate canal which becomes ciliated; the funnel-cell divides into a group of ciliated cells situated on the anterior face of the dissepiment which form the funnel, and the organ becomes fully functional long before the young worm is hatched. I have not attempted to follow in detail the histological differentiation.

*The Setæ.*—The setigerous glands of the inner or ventral series arise opposite the nephric cord in regular alternation with the nephridia, and transverse and longitudinal sections clearly demonstrate the fact that they take their origin in the nephric cords. In Fig. 86 the outer end of the nephric rudiment appears to turn upwards and backwards so as to adjoin the fun-

nel of the succeeding nephridium. In favorable longitudinal sections this appearance may be followed from somite to somite, so that the series of nephridia appears to form a continuous cell-cord thrown into S-shaped undulations. On following the series forward, the group of cells marked *s.gl.* in Fig. 86, which lies between two succeeding nephridia, becomes enlarged, projects into the coelomic cavity, is surrounded by a mesoblastic investment, and a seta is developed in its interior (Figs. 85 to 88, and Fig. 93). The first seta is soon followed by a second, and the two soon force their way through to the outside. The mesoblastic investment persists and gives rise to the muscles of the setæ. The setigerous glands of the inner series therefore grow forth from the nephric cords in regular alternation with the nephridia, and are accordingly of ectoblastic origin, being derived from the middle stratum of the germ-bands.

The outer setigerous glands arise from the middle stratum of the germ-bands, lateral to the nephric cords, as solid ectoblastic invaginations invested by mesoblast precisely like those of the inner series. There can be little doubt that they arise from the lateral cell-cord where this is present, though I have been unable to demonstrate this, owing to the early disappearance of the line of demarcation between the lateral and nephric cell-cords.

Several interesting questions suggested by these facts may be briefly pointed out at this point. If, as I suspect, the lateral teloblast be in reality a setiblast, an interesting side-light is thrown on the affinities of the Hirudinea, for the lateral teloblast of *Clepsine* is certainly homologous with that of *Lumbricus*, and its existence would seem to indicate the former possession of setæ by these animals. It is an interesting fact, secondly, that the nephric cord is double, while the lateral cord is single, and it is not impossible that one of the so-called nephroblasts may in reality be a setiblast like the outer teloblast, though it is not possible to distinguish certainly the setigerous from the nephric elements of the so-called nephric cord until a comparatively late stage. In any case the origin of the setigerous glands, while showing a very remarkable and interesting specialized development, is entirely in accordance with the results of Kleinenberg, Vejdovsky and others as to their ectoblastic origin.



## PART III.

## GENERAL QUESTIONS.

There is reason to believe that *Lumbricus* is a somewhat specialized form, both anatomically and embryologically, and it is therefore necessary to be cautious in drawing general conclusions from the phenomena of development, especially in respect to their phylogenetic significance. Yet the very fact of secondary modification having taken place gives value to a comparison of the development of *Lumbricus* with that of other annelids, since it gives in some degree a test of the weight that can justly be assigned to the various features of the ontogeny.

I may recall the well-known fact that among the annelids, as among many other animals, two types of development occur, which Balfour has conveniently designated as the *larval* and the *foetal* types. The former, represented typically by the development of *Polygordius*, *Eupomatus*, etc., is indirect, and is characterized by the appearance of a free-swimming Trochosphere stage, in which the trunk is more or less completely suppressed and the head-region is highly developed. The second or foetal type occurs in forms like *Lumbricus*, *Criodrilus*, *Clepsine*, etc., which undergo a direct development within an egg-capsule, surrounded by nutritive albumen. In this type the development is abbreviated, the free-swimming stage is more or less completely suppressed, and the trunk-region is early developed. [Hatschek has pointed out that the foetal forms may be arranged under two divisions, one including those like *Lumbricus*, which have little deutoplasm in the ovum and develop by embolic invagination; the other comprising such forms as *Euaxes* or *Clepsine*, in which the ovum is heavily laden with deutoplasm and the gastrulation is consequently of the epibolic type.]

It is furthermore generally agreed that both the larval and foetal forms have undergone more or less extensive secondary modification, the former through adaptation to the conditions of free-swimming larval life, the latter through simplification and abbreviation caused by the lack of those conditions, and perhaps by special adaptations caused by the peculiar mode of nutrition. In view of these facts it seems clear that agreement in any feature of development between the larval and foetal types may

be taken to indicate with considerable probability the primitive character of such a feature, and that, conversely, those features in which the two types differ are due to secondary modification having taken place in one or both forms. Obvious as this principle appears, its importance seems to me not to have been sufficiently recognized in a number of recent papers on the subject, and it must carefully be kept in view in the following discussion.

#### XI. RELATIONS OF THE HEAD<sup>1</sup> (*Prostomium*) AND TRUNK.

The most fundamental question of annelidan morphology concerns the relation between the head and the trunk. Indeed, it is not too much to say that this question, involving as it does the interpretation of the Trochosphere, of the teloblasts, and of metameric segmentation, is one of the most important problems of comparative morphology, though it is admitted by a number of leading morphologists to be incapable at present of more than a conjectural solution. The limits of this paper do not permit a review of the very extensive literature on the subject, and I shall therefore refer at this point to only two of the latest papers. Fraipont has given in his monograph of *Polygordius* (No. 15) an admirable review of recent discussions of the Trochosphere, to which Whitman (No. 52) has added an important discussion of the teloblasts and of growth by concrescence, — questions which were not specially considered by Fraipont. Both these authors admit that the Trochosphere larva of annelids still remains (to use Whitman's phrase) a morphological puzzle, which can only be solved by further extended investigation — an admission which is fully justified by the diametrical opposition of the views of leading authorities on the subject. It would therefore be profitless to enter upon an exhaustive discussion, and I wish only to make a few suggestions in regard to certain points which do not seem to me to have been sufficiently considered and on which a certain amount of light is thrown by the development of *Lumbricus*. They must, however, be introduced by a short review of the general question.

<sup>1</sup> I shall use the word "head" to designate that part of the body (often called prostomium, præ-oral lobe, or cephalic lobe) that contains the anterior median unpaired cavity that lies in front of the first dissepiment, and obviously represents the principal cavity of the Trochosphere.

Either the Trochosphere larva of annelids is the larval representative of an ancestral non-metameric form, as held by Hatschek, Kleinenberg, and Whitman, or it is a purely secondary form as held by Lang and Sedgwick. Under the former view the head must be regarded as phylogenetically the oldest part of the animal, and the trunk as a neomorph, the origin of which involved the origin of metamerism. According to the second view, head and trunk are but secondarily differentiated parts of the ancestral body, and the retardation or rudimentary condition of the metameric trunk-region that now characterizes the Trochosphere is due to cenogenetic changes; thus the origin of metamerism may have been antecedent to the appearance of the Trochosphere, and the head not phylogenetically older than the trunk.

There is no means of deciding between these two conflicting views save by a thorough investigation of the actual anatomical and embryological relations between the head and trunk—a question which I shall now briefly review.

The head has been asserted to differ morphologically from the trunk in the following principal characters: (1) in containing no reproductive organs; (2) in arising from a pair of mesoblastic foundations that arise independently of the trunk mesoblast; (3) in containing an unpaired cavity (“primary body-cavity”) which is the remains of the blastocœl traversed by mesenchymatous cells, and not homodynamous with the cœlomic cavities of the trunk (“secondary body-cavity”), since these arise by cleavage of the mesoblast and are surrounded by mesothelial walls; (4) in possessing a nervous system (Scheitelplatte, of Hatschek, or apical neural plate) which is primitively unpaired (Hatschek), and arises independently of the ventral chain (Kleinenberg, Salensky, etc.).

Let us examine these statements. The first may be set aside, since many of the trunk somites are sterile like the head. The second has been disproved so far as the *Chaetopods* are concerned, by Hatschek, who has clearly shown that the head-mesoblast arises by the forward growth and union of the two mesoblastic trunk-bands, a conclusion which Kleinenberg likewise reached in his later studies (*Lopadorhynchus*), and with which my own observations entirely agree.

The third statement is true as far as the unpaired character

of the head-cavity is concerned, but the other points are of secondary importance. In *Polygordius* and the other larval types the head-cavity is manifestly derived from the blastocœl and is always unpaired. My observations on *Lumbricus* leave no doubt that the head-cavity is median and unpaired in the foetal types also, and except for its very small size has precisely the same morphological character as in the larval types. [This result is entirely opposed to the observations of Kleinenberg, — which have been especially emphasized by Balfour, — according to which the head-cavity in *Lumbricus* arises by the fusion of a pair of lateral cavities apparently homodynamous with *trunk-cavities*.] The mesenchymatous character of the cephalic mesoblast is obviously of secondary importance; for it has been shown that its cells not only have a common origin with those of the trunk-mesoblast, but also extend throughout the trunk-region (migratory mesoblast). Kleinenberg has shown, moreover, that in *Lopadorhynchus* and some other Polychæta the splanchnic mesoblast is formed by a process essentially identical with the formation of the cephalic mesoblast, — *i.e.* by migration of the cells through the blastocœl and their secondary arrangement in a continuous layer, — and he has thus also proved that the relations of the cephalic cavity to the blastocœl afford no ground for Hatschek's distinction between primary and secondary body-cavity. I may add that the same conclusion is reached by the study of the foetal types (though on a very different basis from that adduced by Kleinenberg), for in these forms the blastocœl completely disappears, and the head-cavity is a new formation. In the larval types the coincidence of the head-cavity with the blastocœl is an incidental result of the circumstance that the blastocœl is large and persistent while the cephalic mesoblast is of late origin and is never sufficiently developed to fill the space between ectoblast and entoblast. This coincidence has no more significance than the coincidence of the blastocœl with the archenteric cavity which occurs among certain Amphibia.<sup>1</sup>

The fourth statement requires careful consideration. As far as *Lumbricus* is concerned, it is untrue in both particulars; for the halves of the cephalic ganglion arise at the anterior ends of neural rows, quite separate from each other, but in direct con-

<sup>1</sup> See O. Schultze, No. 40.



tinuation with the foundations of the œsophageal commissures and of the ventral chain. As regards the first point, Kleinenberg's failure to observe the double foundation of the cephalic ganglia seems to have been due simply to his not having studied sufficiently early stages; for the earliest stage he figures is already as far advanced as that shown in Fig. 79 of this paper, in which the two ganglia have already fused.

On anatomical grounds there is considerable reason to believe that the cephalic ganglionic mass was primitively unpaired, as it still remains in *Protodrilus*, and that its bilobed character in the higher forms is the result of the bilateral differentiation of the head (paired sense-organs, etc.). Hatschek endeavored to show that a median unpaired foundation (Scheitelplatte) for the cephalic ganglion was characteristic of annelidan development generally (as typically shown in the development of *Polygordius*), and that this apical plate represented the central nervous system of the ancestral Trochozoön. A comparison of the actual development of the various forms, however, not only shows a marked divergence between the foetal and larval types, which might have been expected, but also indicates that both types must be more carefully examined before any trustworthy conclusion can be reached in regard to the apical plate. As regards the foetal types the evidence is conflicting, but on the whole appears at present to indicate a double foundation for the cephalic ganglia. The facts in *Lumbricus* seem to admit of no doubt, and agree with Kennel's observations on *Ctenodrilus* (No. 26) — a form which possesses a very primitive nervous system. In the case of *Criodrilus*, as Bergh has pointed out (No. 5), Hatschek's earliest figures (No. 18) show the apical plate as a distinctly bilobed structure, though he describes it in the text as median and unpaired. Vejdovsky positively asserts the unpaired character of the apical plate in *Rhynchelmis* (No. 44); but, as he expressly states, he did not observe the apical plate until it had become a large mass, entirely filling the cephalic cavity, and we have seen that in *Lumbricus* the double character of the foundation is only manifest at a much earlier period.

As regards the larval types, all observers agree that the foundation of the cephalic ganglia arises in connection with an unpaired sense-organ ("Sinnesplatte"), which is usually median, but sometimes asymmetrical (Kleinenberg, Salensky). The

apical plate (Scheitelplatte) is primitively the central organ of this sense-organ, and most observers agree that it is likewise median and unpaired. Kleinenberg's remarkable studies on *Lopadorhynchus* and certain *Phyllodocidæ* demonstrate, however, that in these forms the nerve-cells connected with the apical sense-organ form only a comparatively small part of the cephalic ganglia, the greater part being formed from several completely separate paired foundations. Kleinenberg's observations, moreover, afford considerable ground for regarding the apical plate itself as having been primitively a paired organ; for in *Lopadorhynchus* it lies from the first on the right side, and in the corresponding position on the left side is a group of cells that soon disappears, and is suspected by Kleinenberg to represent a degenerate left apical plate. No other observer has studied the origin of the cephalic ganglia in the larval types with any approach to the thoroughness and care that characterizes Kleinenberg's work, and until a more adequate study of the apical plate has been made in other larval types, its morphological significance must remain in doubt. On the whole, therefore, it appears that no trustworthy basis for any fundamental morphological distinction between head and trunk can at present be found in the mode of development of the cephalic ganglia. The adult cephalic ganglia in higher annelids certainly are paired, and it would seem that their mode of origin (whether from a paired or unpaired foundation) depends simply on the time at which the bridge of neural tissue between the two halves is formed, and this time is shown by the facts to be variable.

As regards the second point, Kleinenberg lays great stress on the supposed independent origin of the cephalic and trunk ganglia, which he interprets (in accordance with the theory of development by substitution), as follows: The ring-nerve of the prototroch represents the ancestral central organ, and is the homologue of the ring-nerve of a medusa. In connection with it, in the course of the ancestral development, arose separately the cephalic ganglia in front (umbrellar region) and the ventral trunk-chain behind (sub-umbrellar region), the ring-nerve at first forming the connecting link between them, but subsequently disappearing in the adult and appearing only in the larva (Trochosphere). In the fœtal types the ring-nerve has disappeared even from the larval stages, and the cephalic ganglia

and the ventral chain are, therefore, at first not connected with each other.

This explanation is extremely ingenious, but I must point out the fact that the separate origin of the cephalic ganglia and the ventral chains in the foetal types is by no means an established fact, and that, even if it were, it would be capable of a much simpler interpretation. Hatschek has always maintained the direct and primary connection of the apical plate with the ventral nerve-chain, and this view is supported by Vejdovsky's observations on *Rhynchelmis* and my own on *Lumbricus*. In *Lumbricus* the cephalic foundations are from the first in continuity with those of the ventral chain, though the œsophageal commissures are represented only by rows of neural cells, which are still fused with the general ectoblast, and would scarcely be recognizable were it not for their connection with the neuroblasts. In later stages the commissures lag somewhat behind the other parts, and may thus easily be overlooked. It appears, therefore, as Hatschek has pointed out (No. 20, p. 72), that the entire question as to the separate or common origin of the cephalic and trunk ganglia relates simply to the period at which the œsophageal commissures are differentiated; and the possibility of secondary acceleration or retardation in these structures certainly cannot be denied in view of the fact that in many other metameric animals, entire somites in the middle region may lag far behind other parts, or even be suppressed for a long time — as for instance in the Decapod zoëa.

To sum up, it appears from the foregoing discussion that the only certain embryological ground for maintaining the contrast between the head and trunk lies in the fact that the head-cavity is unpaired, while the trunk-cavities are paired; and this I believe to be a real, though not a fundamental distinction. The fact that the foetal and larval types agree in this respect indicates its primitive character, and this conclusion is, moreover, so strongly supported by the facts of comparative embryology that no one would have called it in question but for Kleinenberg's account of its development in *Lumbricus*.

All the evidence seems to show, therefore, not only that the cephalic cavity is unpaired, but that this is an ancestral feature of the annelid body. But the evidence appears to me to indicate, furthermore, that the head-cavity is to be regarded as homo-

dynamous, not with the double cavity of a single somite, but with *one of the pair of cavities, by the fusion of which each coelomic cavity of the trunk arises*; in other words, the coelomic cavities, with their mesoblastic walls, can be most simply and accurately conceived as forming an elongated ring, the two halves of which lie at the sides of the alimentary canal, and are connected in front by the head-cavity, the walls of which become differentiated into the parts of head.<sup>1</sup> Can this be regarded as a characteristic of the ancestral body? If so, the retardation of the trunk-region in the larval Trochosphere is obviously a secondary feature of development, and the head cannot be regarded as older than the trunk. Under this view, moreover, it would follow that the concrescence of the mesoblastic and neural bands that is so striking a feature of annelidan development must be regarded as an ancestral feature, and not as the result of secondary changes caused by special embryonic conditions. This question I shall now briefly discuss.

## XII. CONCRESCENCE AND THE BLASTOPORE.

We are indebted to Whitman for a most interesting analysis of the phenomena of concrescent growth in the annelid embryo, the process being conceived as a secondary feature of development, brought about by accumulation of deutoplasm in the ovum. His general conclusions (in respect to *Clepsine*) are stated in the following passage (No. 52, p. 175; the italics are mine):—

“ Among the more important differences remaining to be noticed are those which have been brought about under the influence of the food-yolk. The process of gastrulation, the form of the blastopore and its relations to the mouth, have been very profoundly modified in this way. The trunk-bud of the foetal Trochosphere has been carried far from its original post-oral position; and, as the result of this displacement, we see the halves (germ-bands) of the trunk (*which develop side by side as a unit in the larva*) formed separately and carried over the

<sup>1</sup> I may point out the fact that the coelom of annelids is generally agreed to be primitively divided by dorsal and ventral mesenteries into right and left cavities, though the dorsal mesentery often disappears; and that the discovery of the excretory organs of the head has still further lessened the supposed contrast between head and trunk.



massive sphere of yolk in such a manner as to meet along the median ventral line. *This whole process of circumcrescence and concrescence has arisen secondarily, in adaptation to foetal conditions that do not exist in the larval form.* The blastopore, if we include the space traversed in the closure of the germ-bands, has been stretched out of all proportion to its original dimensions, so that it no longer represents the primitive Gastrula-mouth, but merely a secondary prolongation of it backwards along the whole ventral line of the body. In the embryonic Trochosphere we find the blastopore already closed before the trunk-bud begins to develop; hence the line of closure ("Gastrula-raphé") is limited to the ventral line of the Trochosphere. As the metameric body-region is not yet developed, it is evident that the posterior limit of the primitive blastopore falls within the non-metameric region, from which the head-segment of the adult animal is formed."

Concrescence, as thus conceived, is, therefore (to use Professor Whitman's own expression), a process of restoration, by which the two halves of the embryo, which have been mechanically separated by the backward extension of the blastopore along the median ventral line, are brought together again. But a broader examination of the question demonstrates the inadequacy of this explanation, clear as it at first sight appears to be. It is perfectly obvious that the history of the mesoblastic and neural elements in *Lumbricus* is essentially the same as in *Clepsine* and other epibolic foetal types. In both the mesoblastic and neural bands are at first widely separated throughout the middle region of the trunk, and subsequently undergo a process of union along the median ventral line. *Lumbricus* differs only in the acceleration of the ectoblastic part of the germ-bands, which outstrips the other elements and thus closes in the blastopore while the neural and mesoblastic elements still lie quite at the sides of the embryo. Yet the embryo contains very little food-yolk; the gastrulation is of the embolic type, and hence the separation and subsequent concrescence of the germ-bands cannot be explained under Whitman's view, unless we suppose the gastrulation to be a secondary derivative of an epibolic form.

In view of such a possibility, however, let us waive the case of *Lumbricus* and consider the typical larval types. No one can compare the history of the mesoblastic bands in *Clepsine*, in

*Lumbricus*, and in *Polygordius*, without perceiving that it is essentially the same in all, though in *Polygordius* the ectoblast extends over the ventral surface at an even earlier period than in *Lumbricus*. In all, the mesoblastic bands lie at an early period on opposite sides of the body throughout the trunk-region, and their subsequent growth and union along the median ventral line in *Polygordius* and the other larval types is closely similar to the corresponding process in *Lumbricus*, and scarcely less striking than in the epibolic types. There is, however, no food-yolk (*Eupomatus*, *Hydroides*), the gastrulation is of the embolic type, the blastopore never actually extends between the mesoblastic bands (since they are still undeveloped at the time of its closure), and their wide separation must be due to some other cause. The essential agreement in the history of the mesoblastic bands between forms so different both in structure and in the conditions of embryonic development as *Clepsine*, *Lumbricus*, and *Polygordius*, is very strong evidence that mesoblastic concrescence has some ancestral meaning, and was not originally caused, though afterwards it was undoubtedly in many cases modified and rendered more conspicuous, by accumulation of food-yolk in the ovum.<sup>1</sup>

All of the evidence seems, therefore, to indicate that the mesoblast (with the contained cœlomic cavities) originally lay in two masses that extend along the sides of the alimentary canal and joined in front of the mouth and also at the posterior extremity. Concrescence is the ontogenetic repetition of the process by which these originally separate masses extended dorso-ventrally around the archenteron and fused in the middle line, and the explanation of this process must, I believe, be sought in the relation of the germ-bands to the blastopore.

The posterior limit of the ventral surface of the embryo *Lumbricus* may be placed at the point of union of the two primary mesoblasts, and the anterior limit at the mouth. The blastopore, therefore, occupies at first nearly the whole ventral surface, its anterior lip corresponding with the anterior lip of the mouth, its posterior lip lying just anterior to the primary mesoblasts. In

<sup>1</sup> I am aware that I have used the word "concrescence" in a somewhat broader sense than that employed by Professor Whitman. The word, however, cannot logically be restricted to such cases as those of *Clepsine*, and to make such an arbitrary limitation would be simply to ignore the real problem to be solved.

*Eupomatus* the blastopore, though smaller, has the same position, and in both forms it closes from behind forwards, the foremost portion persisting as the mouth. The blastopore also has the same position in the epibolic types (*Clepsine*, *Euaxcs*, etc.), though, as Whitman has shown, its mode of closure has been modified through the enormous accumulation of food-yolk in the entoblastic part.

A comparison of Figs. 35 to 44 will show that the mesoblastic and neural elements of the germ-bands in *Lumbricus* may be most clearly conceived as forming a longitudinal ring surrounding the region of this primitive blastopore, and that concrescence of the germ-bands takes place throughout the middle region of this ring along the line of union of the lips of the blastopore, though these relations are somewhat obscured by the fact that their various elements do not develop at the same rate and the neural ring remains incomplete. Thus the anterior part of both the mesoblastic and neural rings is only completed after the blastopore has narrowed to form the mouth, and the extreme posterior part of the neural ring appears never to develop.

This view of the relation of the germ-bands to the blastopore, taken in connection with the arguments in favor of the primitive character of concrescent growth, points unmistakably to that hypothesis as to the ancestral history of the blastopore first suggested, as far as I am aware, by Bütschli (No. 10), and afterwards developed at length by Sedgwick in his well-known paper on the origin of metameric segmentation (No. 41). In spite of the strong opposition with which this hypothesis has been received in some quarters, and in spite of the difficulties which it, in common with every other theory, has to encounter, it nevertheless appears to me to be the only one that gives any approach to an explanation of the phenomena in question. If we suppose the annelid blastopore to have given rise originally to both mouth and anus by closure in the middle region (as it still does in *Peripatus*), and that this process represents approximately the phylogenetic origin of mouth and anus from the ancestral protostome, the explanation of mesoblastic and neural concrescence becomes obvious. The primitive mode of closure of the blastopore itself has been modified,—probably through the need of a very early establishment of the mouth,—so that the con-

crecence of its lips outstrips that of the other elements of the germ-bands, and the anus is retarded in development. Concrecence of the neural and mesoblastic elements, however, still follows the original mode of development, the lateral parts of both rings long remaining separate behind the point where the germ-bands diverge. The long continuance of this divergence of the germ-bands behind, which is a remarkable feature in the development of many if not all annelids, seems to be due to the retention in this region of the embryonic condition to allow the continued growth and elongation of the body.

The most obvious objection to this view lies in the fact (first pointed out by Hatschek, as far as I am aware) that the proctodæum arises outside the mesoblastic ring (*i.e.* apparently behind the primary mesoblasts) and, therefore, not in the region of the blastopore. This objection is, however, by no means a fatal one, either in respect to the relation between anus and blastopore or to that between the anus and the mesoblastic ring. The first point has been fully considered by Sedgwick in his general discussion, and the differences between the foetal and larval types in this respect show that the development of the anus has been greatly modified. The second point loses much of its force from the facts, first, that the position of the primary mesoblasts is variable (compare *Criodrilus*, in which the mesoblastic ring is not closed behind and the primary mesoblasts are widely separated from each other, or *Eupomatus*, in which the mesoblasts lie at one period on either side of the anus); and second, that upon the breaking up of the primary mesoblasts, which takes place in *Lumbricus* just before the invagination of the proctodæum, the mesoblastic bands grow around the proctodæum and join in the middle line above it. Hence it cannot be denied that the present position of the anus outside the primary mesoblastic ring may be due to secondary changes having occurred in the position, either of the anus, of the ring of mesoblast, or of both.

### XIII. THE TROCHOSPHERE AND THE TELOBLASTS.

It is obvious that if the foregoing interpretation of the annelid embryo be accepted, the Trochosphere cannot be regarded as a primary larval form (representing an ancestral "*Trochozoön*"), but as one which has undergone very great secondary modification through retardation of the trunk-region accompanied by early and special differentiation of the head. That it is such a secondary form, appears to me to be practically demonstrated by the teloblasts which are so marked a feature of the larva. Probably no one will maintain that these remarkable structures are ancestral in the sense of having ever existed as functional adult organs. Physiologically they are specially differentiated growth-



centres, precisely analogous to the apical cells of plants, and like them adapted to facilitate a rapid and continuous elongation of the body in one direction. Morphologically they must be taken to represent parts that have been retarded in development, and at the same time extremely reduced and concentrated by a precocious segregation of material. In other words, the teloblasts represent the rudimentary trunk of the Trochosphere, and indicate the former presence in the larva of a developed trunk, which is now temporarily reduced in favor of the head, the latter having meanwhile acquired special larval organs of locomotion and sensation. The evidence at our command appears to me to indicate that the annelid Trochosphere is a secondary larval form analogous in its mode of origin to the Crustacean Nauplius, which was itself so long regarded as an ancestral form. It is now generally admitted that the former conception of the Nauplius is no longer tenable,<sup>1</sup> and that the characteristic features of the Nauplius are of purely secondary origin, a few anterior somites having been accelerated and specially differentiated to meet the requirements of larval existence, while the others have been retarded or for the time being entirely suppressed. I can see no valid reason against regarding the Trochosphere as having arisen by an analogous process from an elongated segmented ancestral form, the head-region or prostomium being enormously developed and provided with special organs of sense and locomotion, and the trunk-region more or less retarded, becoming reduced, it may be, to a mere trunk-bud, as in the typical larval forms. It is no doubt an astonishing fact that the entire mesoblastic trunk-region of an animal should have been compressed into a single pair of cells, but it is scarcely more astonishing than the complete secondary suppression of the long posterior metameric trunk-region in the Nauplius.

It is instructive to notice that, as regards the retardation of the trunk-region, a series exists among the annelids, which is, broadly speaking, analogous to the series occurring among Crustacean larvæ. *Lumbricus* stands midway between *Polygordius* or *Eupomatus* on the one hand, and *Euaxes* or *Clepsine* on the other. In the latter the mesoblastic bands are fully established, and join in front long before the epibolic gastrulation is com-

<sup>1</sup> For reviews of this question, see Claus, No. 13, and Dohrn, No. 14.

pleted. In *Lumbricus* the germ-bands are present in the gastrula, but are relatively much less developed than in *Clepsine*, and they do not unite anteriorly until after the establishment of the mouth. In *Eupomatus*, finally, the mesoblastic bands are wholly rudimentary at the time the blastopore closes, but they are nevertheless represented by the primary mesoblasts.

I am not prepared to discuss the case of *Lopadorhynchus* and allied forms in which no teloblasts have been observed, for it is very far from certain that they are not really present (see p. 443), and their very general occurrence in the Trochosphere indicates at present that they are to be regarded as characteristic of the larva.

To sum up: as far as our knowledge goes, the development of *Lumbricus* can be most simply and clearly interpreted in accordance with Sedgwick's hypothesis, as follows: (1) The ancestral form possessed an elongated ventral blastopore that gave rise to both mouth and anus by closure in the middle region; (2) the mesoblast and the nervous system originally formed a ring around this blastopore, subsequently undergoing concrescence throughout its middle portion as the blastopore closed; (3) the coelomic cavities were arranged in a continuous series in the mesoblastic ring, each lateral cavity lying opposite a corresponding cavity on the other side of the body, and a single anterior cavity lying in front of the mouth and giving rise to the head-cavity; (4) the larval Trochosphere is secondarily derived from such a form by retardation or temporary suppression of the trunk-region and early and extensive differentiation of the head-region.<sup>1</sup>

Further than this I shall venture no conjecture as to the character of the adult ancestral form, except to state that the views suggested are reconcilable with the derivation of annelids either directly from Cœlenterata, or from Platyhelminths, in accordance with the views of Balfour and Sedgwick, or Lang. The essential feature of all these views is the identification of the principal or longitudinal axis of the body with one of the

<sup>1</sup> The apparent non-extension of the blastopore into the trunk-region in the larval Trochosphere is under this view owing simply to the rudimentary condition of the trunk at the time the blastopore is formed. The early closure of the blastopore is probably due to the advantage of the earliest possible establishment of the mouth in the free-swimming larva, which must procure its own food.

transverse axes of the gastrula, and hence of the Cœlenterate ancestral type, which the gastrula in some degree represents; and we owe to Balfour the fruitful suggestion that the nervous system of the Bilateria may have arisen directly by the elongation of the circum-oral ring of the ancestral form. Kleinenberg has shown in the clearest manner that this view is untenable, if, as Balfour supposed, and Kleinenberg himself believes, the Trochosphere is an ancestral form; for the adult nervous system does not arise from the ring-nerve of the larva, and lies at right angles to it. This objection, however, rests wholly on the supposed homology of the Trochosphere ring-nerve with the circum-oral ring-nerve of a medusoid form; and this homology, to say the least, remains to be proven. On the other hand, the adult nervous system, like the larval "ring-nerve," certainly surrounds the region of the blastopore, as I have endeavored to show; and if there is any force in the foregoing argument, the larval "ring-nerve" is essentially a secondary system, developed in connection with a purely larval locomotor organ. The possibility of such an origin is rendered apparent by the fact that *Polygordius*, and presumably other larval types as well (see Fraipont, No. 15), has not one but several (in *Polygordius* six) parallel ganglionated nerve-rings, of which only two supply the locomotor organ, while the others form part of the general umbrellar nervous system.<sup>1</sup>

Grant that the ring-nerve of the Trochosphere is essentially a secondary larval structure, and the objections to Balfour's fundamental conception disappear, though some of the details of his hypothesis must be modified.

#### XIV. MESOBLAST AND CÆLOM.

Our knowledge of the mesoblast in annelids appears at present to be in a very confused and unsatisfactory condition. In all the foetal types (Oligochaeta, Hirudinea), and in many of the

<sup>1</sup> Fraipont (*l.c.*, p. 56) is inclined to regard the fifth nerve-ring of *Polygordius* (which supplies the prae-oral ciliated band, and which alone is provided with ganglion-cells throughout its entire course) as the representative of the ring-nerve of *Lopadorhynchus* and similar forms. Whether this view be well founded or not, the prototrochal nervous apparatus of *Polygordius* differs remarkably from that of *Lopadorhynchus*, etc., both in position and in structure.

larval types (*Polygordius*, *Eupomatus*, etc.), the entire mesoblast arises from a single pair of cells (teloblasts), which appear near the time of gastrulation in the region of the posterior lip of the blastopore, though they may be differentiated before the gastrula stage is reached, as in the foetal types generally. In a number of the larval types, however (*Lopadorhynchus*, *Alciope*, *Asterope*, *Nauphanta*, *t. Kleinenberg*; *Pileolaria*, *Aricia*, *t. Salensky*), it is asserted that there are no teloblasts, and that the mesoblast is split off from the ventral ectoblast, long after the gastrulation is completed. According to Kleinenberg, the mesoblastic and neural elements are separated from the ectoblast in a common basis (ventral plate) which is afterwards differentiated to form a neural plate and a muscle-plate.

It is much to be regretted that neither Kleinenberg nor Salensky has made a minute study of the posterior portion of the germ-bands in surface-view. All of Kleinenberg's illustrations of the histological detail are made from sections, and a careful study of them has not only left me unconvinced in regard to the absence of teloblasts, but has given some ground for the suspicion that he may have overlooked them—a suggestion which I should not venture to make were it not for his previous failure to see the eight anterior teloblasts in *Lumbricus*. Thus he figures large cells with huge nuclei at the posterior ends of the neural foundations in *Asterope* (No. 31, Taf. 14, Fig. 69) and *Alciope* (*l.c.*, Fig. 67<sup>a</sup>), which look extremely like sections of the neuroblasts in *Lumbricus*; and he figures in Fig. 68<sup>a</sup>, in *Asterope*, a group of large cells at the hinder ends of the mesoblastic bands, which, to say the least, deserve further study, for it is possible that the mesoblastic condensation has not gone as far as in *Lumbricus*, and that the two primary mesoblasts of this form are represented in *Asterope*, etc., by a larger group.

The apparently ectoblastic origin of the mesoblast in forms under consideration, is by no means irreconcilable with the facts observed in the foetal types, though further researches are required to show their precise relations. The explanation must, I believe, be sought in the relations of the posterior ends of the germ-bands to the blastopore, a more precise study of which in the Polychæta is now of the greatest importance. All the evidence goes to show that the primary mesoblasts arise on either side the median line, near the posterior (ventral) lip of the



blastopore, though owing to an acceleration of development, they may be already differentiated in the blastula. After the narrowing of the blastopore, this position is found to be anterior to the anus (apparently latero-ventral) on either side the median line — *a position which very nearly corresponds to the seat of mesoblast-formation at the hinder ends of the germ-bands in Lopadorhynchus and similar types.* There can be little doubt, therefore, that further study of the matter will show the germ-bands of *Lopadorhynchus*, and its embryological allies, to have nearly the same relation to the blastopore as in the other types, for the evidence tends to show that the blastopore of all annelids occupies at first the entire ventral surface. The seat of mesoblast formation has, however, shifted slightly, having passed outward from the lip of the blastopore, so as to lie, *after closure of the blastopore*, in the ectoblast, and the apparent effect of this change has been heightened by a retardation in the formation of the mesoblast. Evidence is not wanting that precisely such a shifting has taken place in other animals, usually, however, in connection with the formation of a primitive streak, by coalescence of the lips of the primitive blastopore. Such a case is that of *Phoronis* (Caldwell, Nos. 11, 12), which is of special value in this connection, since the primitive blastopore has the same position as in annelids, closes in the same manner, and there can be no question of the mesoblastic shifting. The blastopore narrows to form the mouth, as in *Lumbricus*, but a median ventral "primitive streak" is left along the line of the closure, where the layers remain for some time in fusion. The mesoblast arises from three distinct centres of growth situated along the primitive streak, but differing in their relation to it. The anterior part is formed within the lip of the blastopore, and hence from the entoblast, the middle part from the lip itself, and hence from the indifferent cells of the primitive streak, the posterior part just outside the lip, and hence apparently from the ectoblast. There can be little doubt that these three modes of mesoblast-formation were originally alike, and were afterwards differentiated by slight changes of position with reference to the lip of the blastopore. It remains to be seen whether a primitive streak can be found in the annelid embryo, but in any case there can be little doubt that the apparent contradiction between the two types of mesoblast-formation in annelid is

due to a similar shifting of the seat of mesoblast-formation with reference to the blastopore.

It appears impossible at present to determine the primitive origin of the material now segregated in the primary mesoblasts, for the extreme condensation of development involved in their origin has completely masked the original mode of development. There is, however, nothing in the history of the teloblasts to preclude the hypothesis that the walls of the cœlomic cavities were originally formed as a series of gut-pouches, as in *Amphioxus*. The primary mesoblasts lie at the extreme posterior limit of the entoblast, and it is not difficult to picture the process by which a series of gut-pouches, successively formed at the posterior part of the archenteron, might be crowded further and further back in development, until the present complete segregation of the mesoblast in a single pair of the cells was attained. (Cf. Hatschek, *Zoologie*, p. 76.) I will only add that if the mesoblastic somites should ultimately be shown to be homologous with gut-pouches, and if my view of the homodynamy of the prostomial and trunk-cavities be correct, the prostomial cavity (*i.e.*, the primary body-cavity of the Trochosphere), would be comparable with an unpaired anterior diverticulum of the alimentary canal (as in *Gunda* and other Platyhelminthes), or with one of the median chambers of the Actinozoa.

It is interesting to recall in this connection Bateson's discovery that the prostomial mesoblast in *Balanoglossus* is actually derived from an unpaired median diverticulum of the archenteron; and the same author has shown that this diverticulum corresponds closely with the anterior diverticulum in *Amphioxus*, though the latter structure divides into right and left chambers at the time of its separation from the archenteron.

BRYN MAWR, PA., June, 1889.

### C. METHODS.

After testing many different hardening fluids, I have found none to compare with Perenyi's fluid, which gives uniformly the best results, both for sections and for surface-views of all stages, and is far superior to picro-sulphuric acid or corrosive sublimate. Flemming's mixture of osmic, chromic, and acetic acids gives very clear differentiation of the middle stratum of the germ-bands after staining with hæmatoxylin, but in most respects it is far inferior to Perenyi's fluid. The embryos were left in the fluid from 15 to 60 minutes,

placed in 70 per cent alcohol for a day, and kept permanently in 90 per cent alcohol.

For permanent staining no method has proved so satisfactory as borax-carminc followed by hæmatoxylin. After being deeply stained in the carmine (12 hours), and extracted in acid alcohol in the usual manner, the embryos were treated with extremely dilute ammoniacal alcohol for a few minutes, to neutralize the free acid, and were then stained in very dilute Kleinenberg's hæmatoxylin (12 hours or more). In case of overstaining with hæmatoxylin, the color may be again extracted with acid alcohol, after which the specimens are again treated with ammoniacal alcohol. This process, following treatment with Perenyi's fluid, gives beautifully clear preparations, which are specially favorable on account of the clearness with which the cell-outlines are shown. It has been found desirable to embed the specimens for sectioning, as soon as possible after hardening, and to reduce the time of immersion in melted paraffin to a minimum (*i.e.*, not more than 10 or 15 minutes).

For surface-views of the germ-bands, the borax-carminc stain should be very deep, and the hæmatoxylin very slight, so as to give the specimen only a purplish color, not a dark blue. The germ-bands are dissected off on the slide, in strong glycerine. This method has, in my experience, given far better results than that of osmic acid followed by Merkel's fluid, so successfully used by Whitman in the study of *Clepsine*.

For the study of entire specimens of the young stages, I have found Perenyi's fluid followed by alcohol, water, very dilute iodine solution, and glycerine, to give results superior beyond comparison to those attained by any other method. The iodine colors the protoplasm pale yellowish brown, the cell-outlines are clearly marked, and the nuclei are stained deep brown. In time, most of the iodine is precipitated in the form of deep brown spheres, which mar the clearness of the preparations, but such specimens may be afterwards stained with carmine, etc., sectioned and mounted in balsam in the usual manner, and give perfect satisfaction, even after a stay of two years or more in the glycerine.

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## EXPLANATION OF PLATES.

*Reference Letters.*

<i>ar.</i> Archenteron.	<i>ms.</i> Mesoblastic cells.
<i>b.</i> Blastopore.	<i>m. ms.</i> Migratory mesoblast.
<i>c. g.</i> Cephalic ganglia.	<i>mc.</i> Muscle-cells.
<i>c. c.</i> Ciliated cells of the ventral surface.	<i>N.</i> Nephroblast.
<i>c. m.</i> Cephalic mesoblast.	<i>Nb.</i> Neuroblast.
<i>c. p.</i> Cleavage pore.	<i>n. c.</i> Neural cord.
<i>cæ.</i> Cœlomic cavity.	<i>np.</i> Nephridium.
<i>d.</i> Dissepiment.	<i>np. c.</i> Nephric cord.
<i>ec.</i> Ectoblast.	<i>æ. c.</i> CEsophageal collar.
<i>en.</i> Entoblast.	<i>p.</i> Proctodæum.
<i>f.</i> Funnel of nephridium or funnel-cell.	<i>p. c.</i> Prostomial or cephalic cavity.
<i>g. b.</i> Germ-band.	<i>s.</i> Seta.
<i>g.</i> Ventral ganglion.	<i>s. c.</i> Segmentation cavity.
<i>i.</i> Investing cells of nephridia.	<i>s. gl.</i> Setigerous gland.
<i>l. v.</i> Lateral vessel.	<i>s. m.</i> Somatic mesoblast.
<i>L.</i> Lateral teloblast.	<i>sp.</i> Splanchnic mesoblast.
<i>l. c.</i> Lateral cell-cord.	<i>st.</i> Stomodæum.
<i>M.</i> Primary mesoblast.	<i>s. z.</i> Schluckzellen or larval excretory organs.
<i>m.</i> Mouth.	<i>v. l. v.</i> Ventro-lateral vessel.
	<i>v. v.</i> Ventral vessel.

## EXPLANATION OF PLATE XVI.

*Lumbricus fœtidus.*

FIG. 1. Unsegmented ovum, surrounded by the vitelline membrane, with two groups of polar cells.

FIG. 2. First cleavage (in the plane of a group of polar cells).

FIGS. 3 TO 5. Four-celled stage, showing the segmentation cavity.

FIGS. 6 AND 7. Two succeeding stages, showing the division of the large cell into two equal parts, followed by a division of one of the three smaller cells.

FIGS. 8 AND 9. Two views of another specimen in the six-celled stage (the individual cells numbered for identification).

FIGS. 10 AND 11. Two views of a seven-celled embryo.

FIGS. 12 AND 14. Three views of an eight-celled stage.

FIGS. 15 TO 19. Various views of a blastula (optical section in Fig. 19), consisting of thirteen cells, showing the entire structure. The protoplasmic prominence marked  $\alpha$ , attached to cell No. 4 (which is probably accidentally caused) serves to orient the embryo.

FIG. 20. Later blastula with a large segmentation cavity but no cleavage-pore.

FIGS. 21 AND 22. Surface-view and optical section of a blastula somewhat younger than the last, showing the cleavage-pore.

FIG. 23. Surface-view of blastula, showing the two primary mesoblasts at the surface.

(All the figures drawn with the camera from preserved specimens. Enlarged 300 diameters.)















## EXPLANATION OF PLATE XVII.

*Lumbricus fatidus.*

FIGS. 24 TO 30. Series of optical sections showing the early history of the mesoblast. Figs. 24, 26, 27 are side views; Figs. 29 and 30 horizontal views; Fig. 28 is an oblique lateral view of the same specimen shown in Figs. 27 and 29. The series shows the gradual enclosure of the primary mesoblasts within the segmentation cavity, the beginning of the mesoblastic cell-rows and the variation of the cleavage-pore, which is absent from Figs. 24, 25, and 30, but present in the others. The mesoblastic rows meet in front.

FIGS. 31 AND 32. Dorsal and lateral views of a blastula in which the flattening preparatory to invagination has begun. The layers are already clearly differentiated, there is a large segmentation cavity, and the mesoblastic rows still meet in front.

FIG. 33. Dorsal view of a slightly later stage (*cf.* Figs. 34, 39, 40, 45, 46), showing the entoblast, the ectoblast in optical section at the sides, the ectoblastic nuclei of the dorsal surface, and the primary mesoblasts.

FIG. 34. Ventral view of the same embryo, showing the entoblast nuclei and the edge of the ectoblast.

FIG. 35. Ventral view of early gastrula (the anterior extremity directed upwards), showing the ectoblast at the sides and below, the entoblast, and the extreme anterior end of the right mesoblastic row in optical section at *m. s.*

FIG. 36. Gastrula, ventral view, showing the blastopore, the anterior ends of the ectoblastic part of the germ-bands (*ec.*), and the nuclei of the flattened cells of the ventral ectoblast.

FIG. 37. Corresponding view of another specimen in which the lateral infolding has advanced more rapidly than in the last, so as to give rise to a slit-like blastopore. (Compare Fig. 42. For actual section of this specimen, see Fig. 52.)

FIG. 38. Lateral view of established gastrula in which the mesoblastic bands have met above the mouth. The left primary mesoblast (*M*) and mesoblastic band (*ms.*) shown. Archenteron and ectoblast in optical section. Limit of ectoblastic part of the germ-band indicated by the faintly drawn nuclei. (Compare Fig. 43.)

FIG. 39. View of flat gastrula (shown in Fig. 33) from the right side, showing the ectoblast, entoblast, and one primary mesoblast in optical section, and also the ectoblastic nuclei of the right side. (For actual sections of the same specimen, see Figs. 45 and 46.)

FIG. 40. The same specimen in transverse optical section, showing the mesoblastic bands (*ms.*) at the sides.

FIG. 41. Surface view from the left side and below, of the specimen shown in Fig. 36. Only the ectoblastic part of the germ-band is shown, except the primary mesoblast (*M*). Ectoblast in optical section at the sides.

FIG. 42. Lateral view of gastrula at about the same stage as Fig. 37, showing the right mesoblastic band (superficial ectoblast not shown).

FIG. 43. Anterior view of the embryo shown in Fig. 38 (slightly diagrammatic), to show the anterior union of the germ-bands above the mouth and their approximation on its ventral side.

FIG. 44. Dorsal view of the embryo shown in Fig. 42, showing the archenteron, the lateral ectoblast, the primary mesoblasts lying in contact in the middle line, and the two mesoblastic rows (*ms.*).

FIGS. 45 AND 46. Longitudinal (actual) sections from a complete series of the embryo shown in Figs. 33 and 39. Fig. 45 is towards the side and shows the right mesoblastic band in nearly its whole extent. Fig. 46 is nearly in the median line, passing through one of the primary mesoblasts. The segmentation cavity has disappeared. The series shows beyond question that the mesoblastic bands are separate in front. No trace of the Schluckzellen can be seen.

(Enlargement 300 diameters. All the figures with the camera excepting Nos. 32, 39, and 40.)













## EXPLANATION OF PLATE XVIII.

(Nos. 47 to 52 and 57, 58 from *L. fatidus*, Nos. 53, 54, *L. communis*, Nos. 55, 56 from an unknown fresh-water oligochaete, the embryos of which are in all essential features like those of *Lumbricus*.)

FIG. 47. Right ventro-lateral view of an embryo at the earliest period in which the mesoblasts and nephroblasts are distinguishable. Right germ-band in surface view, left in optical section. × 300.

FIG. 48. Right lateral view of embryo with completely established germ-bands, showing position of the teloblasts, cell-rows, etc. × 170.

FIG. 49. Ventral view of the same embryo. The germ-bands wholly separate below. (Outlines with camera. Cells diagrammatic.)

FIG. 50. Right lateral view of older living embryo, showing the stomodæum, archenteron, the coelomic and prostomial cavities, developing nephridia, and the dissepiments. The most anterior of these (*d*<sup>1</sup>) form the ventral and later also the posterior boundary of the prostomial cavity. × 170.

FIG. 51. Left lateral view of embryo in the middle period of development. The anterior teloblasts have broken up (see Fig. 63 for diagram of the germ-bands); the primary mesoblasts remain. The dorsal limit of the mesoblast is marked by the lateral vessel (*l. v.*), which ultimately coalesces with its fellow to form the dorsal vessel. × 30.

FIG. 52. Transverse (actual) section through the embryo shown in Fig. 37. The mesoblastic bands are quite distinct from the ectoblast through their whole extent, and are now widely separated in front. × 300.

FIGS. 53 AND 54. Transverse (slightly oblique) section through an embryo at a somewhat earlier stage than Figs. 48, 49. No. 54 (the more posterior) passes through the primary mesoblasts (which appear on the apparent dorsal side owing to the great curvature of the bands) and the two nephroblasts of the left side. No. 53 cuts the left mesoblast (*Nb.*), the left (double) nephric cord, and one of the right nephroblasts. All these teloblasts lie at the surface. × 300.

FIGS. 55 AND 56. Two consecutive horizontal sections through the anterior region of an embryo in which the prostomial cavity has just appeared. In No. 55 (more dorsal) the extreme anterior part of the mesoblast appears, and the bridge of neural tissue (apparently fused with the ectoblast) that joins the two cephalic ganglia. In No. 56 the prostomial cavity appears, lying between the cephalic ganglia. In the following section this cavity disappears, and the dorsal wall of the stomodæum appears. × 300.

FIGS. 57 AND 58. Two transverse sections through the anterior part of an older embryo. No. 57 (the more anterior) shows the prostomial cavity and the dorsal wall of the stomodæum. No. 58 (two sections further down) shows the anterior corners of the anterior pair of coelomic cavities, with the prostomial cavity between them. × 300.

(All the figures with the camera.)















## EXPLANATION OF PLATE XIX.

Fig. 61, *L. communis*; Fig. 62, *L. terrestris*; the others from *L. foetidus*.

FIG. 59. Superficial view of the posterior termination of the neural and nephric cell-rows of the left germ-band, showing the division of the neuroblast.  $\times 700$ .

FIG. 60. The primary mesoblasts and beginning of the mesoblastic rows in a specimen of the same age as the last.  $\times 450$ .

FIG. 61. Superficial view of right germ-band, showing the four teloblasts; the nephroblasts dividing.  $\times 375$ .

FIG. 62. Similar view of left germ-band of *L. terrestris*.  $\times 375$ .

FIG. 63. Diagram of the hinder part of the germ-bands of an embryo in the stage shown at Fig. 51. The bands are spread out flat, and all their elements are shown. The lateral cell-cord cannot be distinguished from the general ectoblast.  $\times 250$ .

FIG. 64. Superficial view of part of the left germ-band of *L. foetidus* to show division of nephroblast. The nuclei of the superficial ectoblast are accurately drawn, and are seen directly to overlie the teloblasts and cell-rows.  $\times 700$ .

FIG. 65. Surface view of the germ-bands at a late stage at the point of divergence behind. Below the horizontal line the focus is quite superficial, in front of it the cells of the various rows are shown, separated here and there by deeper-lying ectoblast cells (*e.c.*). At the right appears the edge of the mesoblastic band (*ms.*) lying at a somewhat deeper level. The lateral cord is indistinguishable.  $\times 400$ .

(All the figures with the camera from preserved specimens.)













## EXPLANATION OF PLATE XX.

*Lumbricus communis.*

FIGS. 66, 67, 68. Three cross-sections from the same series with Nos. 53 and 54 (Pl. XVIII.). Fig. 66 is next to No. 54, and passes through the outer nephroblast on the left side. Fig. 67 is two sections anterior to No. 53, and passes through the right neuroblast and lateral teloblast (one of the nephroblasts of this side is shown in Fig. 53, and the other appears in an adjoining section). Fig. 68 is several sections further forward. × 300.

FIG. 69. Cross-sections through a slightly later stage (*cf.* Fig. 94, Pl. XXII.), showing the cleavage of the mesoblast. × 300.

FIG. 70. Adjoining section from the same series in the region of a dissepiment. × 300.

FIG. 71. Cross-section of germ-bands, a little later than the last. The neural rows are entirely covered by the ectoblast. The nephric rows still lie at the surface. The lateral rows cannot clearly be distinguished. × 400.

FIG. 72. Cross-section through the posterior part of an embryo at about the stage of Fig. 51, to show the dorsal extension of the germ-bands by migration, the middle stratum, the longitudinal muscle-bands, and the longitudinal vascular trunks. × 225.

FIGS. 73 TO 78. Tangential longitudinal sections (somewhat oblique) from a series which shows the entire course of the mesoblastic and neural rows, with the corresponding teloblasts, the origin of the cephalic ganglia, head-mesoblast and Schluckzellen (see p. 415). The right primary mesoblast and the right neuroblast appear in No. 73; the left mesoblast in No. 75, the hinder part of the left mesoblastic band and the anterior part of the right in No. 77; the left mesoblast in Fig. 78, which passes through the middle line in front. × 300; No. 76, × 400.

(All the figures with the camera.)















## EXPLANATION OF PLATE XXI.

Figs. 82, 85, from *L. fatidus*; Fig. 83 from *L. terrestris*; the others from *L. communis*.

FIG. 79. Sagittal section of anterior part of an embryo shortly after the appearance of the head-cavity and the union of the cephalic ganglia. The remains of the Schluckzellen shown at *S.Z.* × 225.

FIG. 80. Corresponding sections through a later stage, in which the first pair of coelomic cavities have come together behind the cephalic cavity at *cæ*, the first dissepiment shown at *D.* × 225.

FIG. 81. Sagittal sections through a still later stage, in which the cephalic ganglia have separated from the ectoblast and begun to travel backwards; the prostomial cavity is nearly filled with a network of mesoblastic cells; the oesophageal gland cells at *gl.* × 225.

FIG. 82. Sagittal section of young embryo of *L. fatidus* to show the thickened lower lip *s. p.* of the stomodæum. × 225.

FIG. 83. Longitudinal section through the nephric cord and developing nephridia, showing their relation to the dissepiments and coelomic cavities. × 400.

FIG. 84. Corresponding section through *L. communis*. × 400.

FIG. 85. Surface view (from within) of developing nephridia and setigerous gland. The lateral limits of the nephric cord are defined by the longitudinal muscular bundles (*m. c.*). × 700.

FIG. 86. Longitudinal section through developing nephridia (somewhat older than in Fig. 84), and setigerous glands, showing their relations to the nephric cords, etc. The section is slightly oblique, and passes in front into a longitudinal bundle of muscle-fibres (*m. c.*) (which now overlaps the margin of the nephric cord). × 400.

FIG. 87. Longitudinal section through still older nephridia. × 400.

FIG. 88. Corresponding section of a later stage, in which the setæ can be distinguished. The nephric cord can no longer be made out in front. × 400.

(All the figures with the camera.)













## EXPLANATION OF PLATE XXII.

Fig. 89 from *L. fetidus*; the others from *L. communis*.

FIG. 89. Surface view of part of the dorsal wall of an embryo in the stage of Fig. 50, showing a few of the large ectoblast cells (or their nuclei), the branching muscle-cells and the amœboid cells (*x*) of the migratory mesoblast. X 400.

FIG. 90. Part of cross-section through posterior part of an embryo of about the same age as Fig. 51, in the region where concrescence of the neural cords is in progress; the section passes through the commissures, and the neural rows are completely separated from one another. X 400.

FIG. 91. Section from the same series two sections behind the last, in the region of a pair of ganglia; the neural rows are connected above by a bridge of neural tissue. X 400.

FIG. 92. Longitudinal section (drawn by combining sketches of two adjoining sections) a little to the side of the one shown in Fig. 80, showing the ciliated canal of the head-kidney embedded in the dorsal wall of the archenteron. X 400.

FIG. 93. Longitudinal section showing the setigerous glands, dissepiments, ventrolateral blood-vessels and portions of the nephridia in a stage about like that shown in Fig. 51. X 300.

FIG. 94. Sagittal section through the posterior part of an embryo (like Fig. 51) shortly before the formation of the proctodæum. The neural rows end abruptly behind, and the primary mesoblasts are the only teloblasts remaining. X 300.

FIG. 95. Section from posterior part of a transverse series of an embryo just before hatching. Owing to the upward curvature of the hinder part of the body, the section passes nearly horizontally through the germ-bands. The mesoblastic bands are in contact at their hinder ends; the lateral cell-rows end abruptly behind. X 225.

FIG. 96. Section from the same series, five sections further forward, cutting the hinder part of the germ-bands transversely and the proctodæal invagination vertically. The primary mesoblasts have disappeared; the mesoblastic bands can be traced around the proctodæum and meet on the dorsal side. X 225.

FIG. 97. Sagittal section (corresponding precisely to No. 94, but a little further toward the side) passing through one of the mesoblastic bands and through the broad proctodæal invagination. The latter is deepest ventrally and fades away towards its anterior lip. The tip of the mesoblastic band represents the former position of the primary mesoblast. X 350.

(All of the figures drawn with the camera.)











# ON THE MORPHOLOGY OF RIBS AND THE FATE OF THE ACTINOSTS OF THE MEDIAN FINS IN FISHES.

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IN a paper read before the American Association for the Advancement of Science, two years ago, I reached the following conclusions on the ribs of vertebrata :<sup>1</sup>—

“ 1. The ribs are developed *between* the myocomata ; they are therefore *intervertebral*.

2. The ribs are originally one-headed and connected with well-developed intercentra.

3. All forms and connections of the other ribs can be derived from that condition.

4. The lower arches of the caudal vertebræ are either formed by true ribs, the oldest fishes (Ganoidei, Dipnoi), or by processes of the intercentra (Teleostei, Stapedifera).

5. The connection between the Dipnoans and the Stapedifera is still missing.

6. Some remarks on the nomenclature of the elements of the vertebral column.

Owen's names, 'neurapophysis' and 'pleurapophysis,' are not correct ; the neural and pleural arches are no processes of the vertebræ, but are distinct parts.

The two elements composing the neural arch ought to be called the *neuroids* ; the two elements composing the pleural arch, the *pleuroids*.

The spines connected with the neuroids ought to be called, as before, *neural spines* ; those connected with the pleuroids, *pleural spines*.

The real centrum of the vertebra ought to be called *centrum* ; the lateral elements composing it, *hemicentra* (Albrecht), not pleurocentra.

The name intercentrum ought to be preserved.”

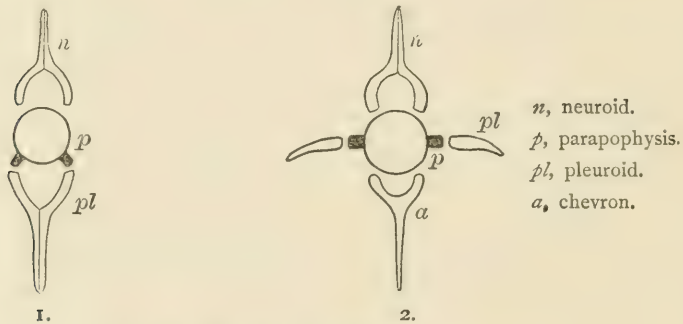
<sup>1</sup> BAUR, G. On the Morphology of Ribs. *American Naturalist*, October, 1887, p. 45.



I have nothing to change in these general results, but can add some important facts relating to numbers 4 and 5.

*The connection between higher vertebrates and fishes is found to be the condition represented by LEPIDOSTEUS.*

Up to this time the difference in the tail of fishes and the higher vertebrates appeared to be a fundamental one. In fishes the "hæmal arches" which enclose the subcaudal blood-vessels are either formed by true ribs, or by the prolonged parapophyses to which the ribs are united. In all higher vertebrates the ribs are entirely separated from the "hæmal arches"; they are placed above these on the side of the vertebræ. The following diagrams represent the two conditions:—



1. Caudal vertebra of Fishes.

2. Caudal vertebra of higher Vertebrates.

It is evident that the "hæmal arch" of fishes, which is either composed of pleuroids, or of pleuroids and parapophyses, cannot be the homologue of the "hæmal arch" of the higher vertebrates. The question is, what elements of the fish's skeleton are used in the formation of the "hæmal arch" of the higher vertebrates; in other words, *what are the homologues of the chevron bones?*

The original condition is, that the subcaudal blood-vessels are surrounded by the pleuroids, in the same way as the neural cord is surrounded by the neuroids. In the higher vertebrates the pleuroids have moved dorsad, and have become entirely independent from the blood-vessels. In fishes the pleuroids are connected with the parapophyses ("Basalstümpfe" Goette) of the vertebra. The condition found in the higher vertebrates could be developed by two different ways: either the parapo-

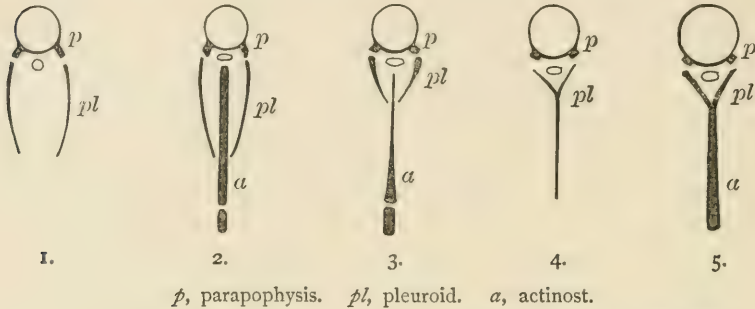
physes move dorsad together with the pleuroids (in this case the chevrons cannot represent parapophyses), or the pleuroids alone begin to move, separating from the parapophyses, which would form the chevrons. The latter opinion was held by me until now. The examination of *Lepidosteus* shows that this view is incorrect. There are forty præ-anal vertebra in a skeleton of *Lepidosteus osseus* L. before me. From the second we find well-developed parapophyses to which strong pleuroids are articulated. In the most posterior vertebræ the pleuroids begin to bend downwards and the parapophyses become a little smaller. The 41st vertebra shows the following conditions: The pleuroids are connected with parapophyses and are directed downwards; *between the two pleuroids a strong element is placed which nearly touches the centrum of the vertebra, and which supports the subcaudal blood-vessels; this strong element is the first well-developed actinost of the anal fin.* It is very strong proximally, differing from the actinosts of other fishes in this regard. In the 42d vertebra we have similar conditions. The second well-developed actinost is below the vertebra supporting the subcaudal blood-vessels, but it is not so strong proximally as the first; the ribs are not directed downwards, but backwards, and are entirely separated from each other. We have about the same characters in the next four vertebræ. In the 43d and 44th the pleuroids are turned backwards. The 43d is connected with one actinost, the 44th with two; the actinosts become very thin proximally, resembling the free actinosts in other fishes. The relation of actinosts and vertebræ becomes loose. There are in all eight well-developed actinosts of the anal fin; the anterior and posterior ones are rudimentary; these eight actinosts are in relation to six vertebræ. In the 45th and 46th vertebræ the ribs begin to turn downwards again, touching each other distally, at the same time they enclose the subcaudal blood-vessels. The same condition we have in all the following vertebræ, in which the distal parts of the pleuroids co-ossify and become very strong. These distal parts contain also the actinosts of the caudal fin.

*The anterior part of the post-anal portion of the tail in Lepidosteus shows the condition of the higher vertebrates, the posterior part that of fishes.*

The Batrachia (Amphibia) developed from forms in which the process, which begins at the anterior part of the post-anal

portion of the tail in *Lepidosteus*, had been carried through the whole tail. The form from which the Batrachia started must have had a continuous anal and caudal fin, with well-developed actinosts free from the ribs. *The chevron bones are the actinosts of this continuous fin.*

The following diagrams show different vertebræ from the posterior part of the vertebral column in *Lepidosteus*:—



1. 40th vertebra of *Lepidosteus*.

2. 41st vertebra of *Lepidosteus*.

3. 43d vertebra of *Lepidosteus*.

4. 48th vertebra of *Lepidosteus*.

5. 53d vertebra of *Lepidosteus*.

*So far it has been the opinion that the elements of the anal and caudal fins of fishes had disappeared entirely in the higher vertebrates; but now we have shown that the elements of these fins do not disappear, but are represented by the chevron bones of the tail vertebræ, which are the partial homologues of the actinosts.<sup>1</sup> The actinosts of the dorsal fin and the upper part of the caudal fin became probably united with the neuroids, and have undergone reduction afterwards. That the anterior and posterior paired fins of fishes, the anterior and posterior limbs of vertebrates in general, are the result of fusion of actinosts of a continuous lateral fin, there seems to be little doubt.*

Sept. 19, 1889.

<sup>1</sup> The proximal part of the chevron above the subcaudal blood-vessels represents the intercentrum, the distal part the actinost. In all higher vertebrates the intercentrum and the actinost are united.

# ON THE MORPHOLOGY OF THE VERTEBRATE-SKULL.

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## I. THE "OTIC" ELEMENTS.

IN this article attempts will be made to show that the doctrine of the "otic" bones established by Professor Huxley twenty-five years ago, and held since that time by nearly all morphologists, is incorrect. The material upon which these notes are based consists of the skulls of *Lepidosteus*, *Amia*, *Necturus*, *Mastodonsaurus*, *Chelone*, *Ichthyosaurus*, *Sphenodon*, *Didelphys*. Taking *Chelone* as a central form, I shall then examine first the higher and afterwards the lower types.

In *Chelone* the foramen magnum is bounded laterally by the exoccipitals; to these bones the paroccipitals (Owen), opisthotics (Huxley) are united by suture on the outside. In front of the paroccipitals another pair of bones is found, the petrosals (Owen), proötics (Huxley). The supraoccipital joins the paroccipitals and petrosals, forming the characteristic Y-shaped figure. Between the paroccipital and the petrosal at the lower side, the stapes is placed, which is small in comparison with the surrounding bones.

In *Ichthyosaurus*<sup>1</sup> we have about the same conditions: the petrosal is a small bone; there are no true sutures between this element, the paroccipital, and supraoccipital, they are all separated by cartilage, which is very much more developed than in *Chelone*. The stapes is exceedingly large, surpassing in size not only the petrosal, but also the paroccipital; it is placed between paroccipital and petrosal below.

In *Sphenodon* we have a corresponding arrangement. In the

<sup>1</sup> My observations on Ichthyosauria are mainly based on the splendid material in the collection of Mr. A. N. Leeds of Eyebury, near Peterborough, England, in which the elements of the skull are separated. I have to thank Mr. Leeds very much for his great kindness and hospitality, shown to me during a visit two years ago.



old animal supraoccipital, exoccipitals, paroccipitals, petrosals, are united, but in the young all these elements are free. There is much cartilage between the supraoccipital and the petrosal and paroccipital. The paroccipital is united to the exoccipital by suture; the elements in question of a young *Sphenodon*<sup>1</sup> resemble those in *Chelone* and especially in *Ichthyosaurus*. In all other Monocondylia the paroccipital is united very early to the exoccipital, forming the paroccipital process of this element. In all, the stapes is placed between the paroccipital and petrosal, and becomes more and more reduced in size. In *Sphenodon* it is of relatively large proportions.

In *Didelphys* the paroccipital is free from the exoccipital, but united with the petrosal. This complex, for which the name "periotic" has been introduced, is suturally united with the squamosal, in which the quadrate and quadratojugal is also contained. The stapes is between paroccipital and petrosal and very small.

Now let us consider for a moment the supraoccipital. According to Professor Huxley this bone in the Monocondylia contains on each side an element which is said to be free in the embryo. In all the Monocondylia (except the Theromora, of which nothing is known as to the point at issue) the supraoccipital receives on each side the upper semicircular canals to a smaller or greater degree; this we find in the lowly organized *Ichthyosaurus* and in the highly specialized Bird. But these canals are not lodged in a peculiar element confluent with the supraoccipital on each side, called *epiotic* by Professor Huxley, but in the *supraoccipital* itself. The part of the supraoccipital containing the canals never develops from a distinct centre of ossification. There is no indication of it in the *Ichthyosaurus* and young *Sphenodon*, in which the supraoccipital is very small. I thought to find this element in the Testudinata, in which the paroccipital remains always free, but in embryos of Cheloniidæ, Chelydridæ, Trionychidæ, Emydidæ, I failed to do so.

In Mammals the upper semicircular canals do not reach into the supraoccipital.

As result of the examination of the skulls of the higher forms

<sup>1</sup> I am very much obliged to Prof. B. G. Wilder, of Ithaca, for a young specimen of *Sphenodon* lent for examination. This animal forms in a half-adult stage a wonderful specimen for a basis of osteological studies.

we may state the following: There are always to be found three elements in connection with the ear, the *paroccipital*, *petrosal*, and *stapes*; the stapes, very large in the lower types (*Ichthyosaurus*) becomes more and more reduced in size, ascending to the higher types. A fourth element, the supraoccipital, takes part in the Monocondylia, but not in the Mammals.

Passing now to the examination of the lower forms (*Necturus*, *Mastodonsaurus*, *Amia*, and *Lepidosteus*), in *Necturus* the foramen magnum is bound by the small exoccipitals; on the outer side of these are the free paroccipitals, then follow in front the large stapes and the petrosal. The same condition can be seen in *Proteus*, the other living representative of the Proteida; but in the other Batrachia the paroccipitals are co-ossified with the exoccipitals.

In the Stegocephalia<sup>1</sup> we have exactly the same: in some of the genera (*Cyclotosaurus*) the paroccipital is free from the exoccipital; in others (*Mastodonsaurus*) it is co-ossified with the exoccipital. The paroccipital is in relation to a dermal plate, which is very improperly called the "epiotic." I propose the name "*paroccipital plate*" for it.

Turning now to *Amia*,<sup>2</sup> we find the exoccipitals very large; on the upper and outer side of these a small bone is seen, which corresponds exactly to the paroccipital in *Cyclotosaurus*; it is also in relation to a dermal plate, and there is no doubt that this small bone is the true homologue of the paroccipital in the Batrachia and higher Vertebrates. Between the extensive petrosal and the exoccipital a large but thin bone is found, the "*intercalare*" of Vrolik.

In *Lepidosteus* the conditions are about the same, but there is no bone between the petrosal and exoccipital, corresponding to the intercalare. If this bone is removed in *Amia*, we have the arrangement of *Lepidosteus*. In *Amia* the paroccipitals take no part in the formation of the semicircular canals, but they do in *Lepidosteus*.

<sup>1</sup> It is to be regretted that my friend, Dr. E. Fraas, did not give much attention to morphological questions in his extensive work on the Labyrinthodontia of the Trias, for which he had a wonderful material at hand; my determinations are mostly based on his text and figures.

<sup>2</sup> My thanks are due to Prof. Ramsay Wright of Toronto for a splendid specimen of *Amia*, presented for examination.

The question now is, what is the homologue of the intercalare? It is absent in all forms in which the cranium is not or only little ossified, the Holocephali, Selachii, Dipnoi, Chondrostei. In *Polypterus*, the living representative of the Crossopterygia, the intercalare appears to be a large element, in which the paroccipital may be contained. I have not examined this form. From the papers of Agassiz, Mueller, and Traquair, I could not form an exact opinion, but from notes and drawings very kindly sent to me by Dr. E. Koken of Berlin, I have reached the conclusion that *Polypterus* is an aberrant form, the morphology of which is not yet fully understood. In the Amiidæ the intercalare appears for the first time, and from this family the "Teleostei" have partially inherited it. Fossil fishes do not throw any light upon this question.

We have seen that in the lowest "Stapedifera" the stapes is largest, and that it becomes more and more reduced in the higher forms. There can be no doubt that the ichthyic ancestors of the Batrachia must have possessed an element corresponding to this well-developed stapes. I think that the intercalare represents this element. The stapes is a true bone of the cranium; it is not formed by any part of the visceral arches in the Batrachia, and all such connections in the higher forms must be considered as secondary. It is possible to understand now why the opinions on the origin of the stapes differ so immensely.

The "tympanic bone" in Mammals has no homologue in the Monocondylia, with the exception of some Birds where a similar structure is to be seen (Psittaci, part); it is very small in the Monotremata and becomes specialized in the higher groups. The opinion of Peters and others, lately defended by Dr. H. Gadow, that the tympanic represents the quadrate, cannot, I think, be adopted. There seems to me to be very little doubt that the quadrate of Mammals is represented by that part of the squamosal to which the lower jaw is articulated, since we have the same condition in the Theromora, which are nearest the ancestors of Mammals.

I append, in a tabular form, the views of Professor Huxley and myself, side by side.

The *paroccipital*, Owen, of fishes is called by Professor Huxley "epiotic," and considered the homologue of the "epiotic" in Labyrinthodontia; the homologue of that portion of the supraoccipital which lodges a part of the upper semicircular canals in the Monocondylia; the homologue of one part of the squamosal in Mammals.

The petrosal of Owen and former authors is called "proötic" by Professor Huxley.

The "intercalare" (Vrolik) in fishes is called by Professor Huxley *opisthotic*, and considered as the homologue of the paroccipital in the Monocondylia.

Aug. 30, 1889.

The *paroccipital*, Owen, of fishes, is the paroccipital in Batrachia and Monocondylia and the "mastoid" portion of the squamosal in Mammals. The paroccipital of the Batrachia is free in the Proteida, but co-ossified with the exoccipital in the other living representatives. In the Stegocephalia it may be free, or united with the exoccipitals. The so-called "epiotic" in the Stegocephalia is only a dermal plate covering the paroccipital, which ought to be named the paroccipital plate.<sup>1</sup>

The supraoccipital of the Monocondylia consists of this element alone, and not of more.

I retain the name *petrosal*.

The "intercalare" (Vrolik) in fishes is the homologue of the stapes in all higher vertebrates, and the name intercalare ought to be used in preference to columella or stapes for all vertebrates.

## 2. THE TEMPORAL ARCHES.

In the oldest Batrachia, the Stegocephalia, we find a continuous dermal covering of the upper and lateral parts of the skull. This covering is interrupted by five openings, — the two nasal openings, the orbits, and the single parietal foramen: the same conditions we have to expect in the ichthyic ancestors of the Batrachia; forms like *Lepidosteus* would express such a stage. The dermal bones of such a skull have been developed from scales, and must have been very numerous at first; later blending of elements, or enlargement of some at the cost of others, took place, and the number was reduced. In the Stegocephalia the number of these dermal ossifications is nearly constant. The bones which interest us in the question about the temporal arches are the following: parietals, frontals, post-frontals, post-

<sup>1</sup> Among the Monocondylia the paroccipital is free in the Ichthyosauria and Testudinata, but united with the exoccipital in the rest.



orbitals, supratemporals, squamosals, jugals, quadratojugals, supraoccipital and paroccipital plates (epiotics). In some of the Stegocephalia another plate is found between the postorbital and the frontal (*Melanerpeton*); this we have to consider as the vestige of one of the more numerous plates of the ancestors of the Stegocephalia.

In the oldest Testudinata we have also a complete bony covering, but the number of elements has been reduced from 22 in *Melanerpeton* to 12 in *Chelone*. There are no distinct postorbitals, supratemporals, supraoccipital and paroccipital plates. This condition we still find in living forms like the Cheloniidæ and Dermochelyidæ. From such forms the Chelydridæ, Dermatemnidæ, Staurotypidæ, Cinosternidæ, Platysternidæ, Emydidæ, Testudinidæ, Trionychia, developed by losing the connection between the squamosal and parietal, — in other words, by losing material from behind. But at the same time a reduction took place from below, between quadrate and jugal. The result was the formation of a more or less slender arch between the orbit and the quadrate. In a few cases this arch became entirely reduced, — *Terrapene*, *Geæmyda*.

In the Pleurodira two kinds of reductions took place; one from below, which destroyed the connection between orbit and quadrate, but retained that between squamosal and parietal. This we see in the Chelydridæ; in *Chelodina* even the connection between squamosal and parietal has gone. The total absence of a temporal arch in *Terrapene* and *Geæmyda* on one side, and of *Chelodina* on the other, is the product of two different kinds of reduction. The first is produced by reduction from below and behind; the other by reduction from below only.

In the Sternotheridæ and Podocnemididæ a reduction takes place from behind and below, as in the Chelydridæ. In none of the Testudinata is a true supra- or infratemporal fossa developed; there is only one arch which represents the whole complex between parietal, frontal, and jugal, quadratojugal.

The complete covering of the skull is for the first time interrupted in the Ichthyosauria and Aëtosauria, by the appearance of a supratemporal fossa, which develops between parietal, squamosal, and the upper posterior border of the orbit. The bony arch below the supratemporal fossa which connects the orbit with the quadrate is now affected in two different ways:

1. The broad single arch remains single, but becomes more and more slender and can be interrupted. Plesiosauria, Theromora, Mammalia, Squamata (Lacertilia, Pythonomorpha, Ophidia).

2. In the broad single arch appears another opening, the infratemporal fossa forming an upper and lower arch which connects the orbit with the quadrate: Rhynchocephalia, the whole archosaurian branch (Crocodilia, Dinosauria, Pterosauria), Birds.

Until now the Squamata had been considered by a large number of anatomists as derived from the Rhynchocephalia, and I have held the same view. The Squamata were looked at as Reptiles, in which the lower temporal arch of the Rhynchocephalia had disappeared. But this is not the case. It seems very much more probable that the Squamata never possessed an infratemporal fossa, but that the broad arch was reduced from below in the same way as in the Testudinata; and that the old opinion of Hallmann, Hollard, Owen, that the squamosal of the Squamata is the homologue of the quadratojugal, and the supratemporal or mastoid of the Squamata the homologue of the squamosal of the Archosaurian branch, is the correct one. In all Reptilia, if no reduction has taken place, there are two elements between quadrate and parietal: the only exception is found in the Ichthyosauria. In these a third bone is inserted, which has to be considered as an original part of the upper bone. The same element is found in the Stegocephalia. In all these forms in which a quadratojugal has been recognized, there is never a "supratemporal" (as seen in the Lacertilia); in all forms in which this supratemporal was found, there is no quadratojugal. From a careful comparison of the skulls of the different groups of Reptilia, I reach the conclusion that the supratemporal or mastoid (opisthotic, Cope) of the Squamata is in fact the squamosal, and the bone called squamosal the quadratojugal.

In the Iguanidæ, Agamidæ, Lacertidæ, Anguidæ, Varanidæ, both bones are well developed; in the Helodermatidæ the squamosal (supratemporal, Parker; opisthotic, Cope) is large, the quadratojugal (squamosal, Parker) very small; in the Ophidia the quadratojugal has disappeared entirely. In the Tejidæ the squamosal becomes reduced and united in some forms with the

quadratojugal. In the Geckonidæ generally only one bone is present; this represents the quadratojugal, the squamosal may be lost entirely or reduced to a diminutive scale. In the Chamæleontidæ the quadratojugal has been greatly enlarged at the expense of the squamosal, which has been almost entirely reduced. In the Rhynchocephalia (Sphenodontidæ) and Chamæleontidæ we have the two extremes of development of these two elements. In *Sphenodon* the squamosal is very large, the quadratojugal very small; in *Chamæleon*, the quadratojugal is very large, the squamosal very small.

In the Plesiosauria, Theromora, and Mammalia, the quadratojugal and squamosal are confluent with the quadrate.

Sept. 15, 1889.

## ON THE POSITION OF *CHAMÆA* IN THE SYSTEM.

R. W. SHUFELDT.

THERE are two species of *Chamæa* in the United States avifauna, — the *C. fasciata*, which is confined to the coast region of California, and *C. f. henshawii*, a variety of the latter which ranges through the “interior of California, including the western slope of the Sierra Nevada.” Ornithologists have bestowed the name of the Wren-Tit upon the first-mentioned of these, while the second one is referred to as the Pallid Wren-Tit. In the absence of any detailed and published account of the structure of *Chamæa*, made comparative with its supposed affines, one would naturally be led to believe, from these names, that the systematists regard these birds as Tits with a tincture of Wren in them; and such, I understand, is generally the case, or otherwise they would certainly have been designated as Tit-Wrens. Several dissenters from this opinion are, however, known to me, and chief among these I would allude to Mr. Robert Ridgway, Mr. F. A. Lucas, and Mr. J. A. Allen. In conversation with Mr. Ridgway on the subject, although he seemed to be disinclined to advance any decided opinion in the premises, he left the impression upon my mind that he regarded *Chamæa* more as a Wren than a Tit, and very kindly allowed me to examine skins of both groups in the collections of the Smithsonian Institution. Among these he was so good as to point out and invite my attention to the external characters in such forms as *Cinnicerthia unirubra* and *Cinnicerthia unirufa*, the first being a species from Ecuador, and the latter from Colombia. He remarked that, in his opinion, these birds were Wrens, and I was struck with their general external resemblance to *Chamæa*, more especially in the case of *unirufa*, which, if I remember, was the species with the longer tail. Both, however, were, upon the whole, unitinted; their heads tufti-crested; a tendency in one for the tarsal scutella to become obsolete; and in the case with



both, the form, size, bill, and general *facies* were considerably like *Chamæa*. It was also interesting to note that these birds had the flight-feathers of the wings indistinctly barred, as we so often find them among certain troglodytine types.

Mr. Lucas has published it as his opinion "that *Chamæa* appears most decidedly to belong with the Wrens, and not with the Titmice." (*Proc. U. S. Nat. Mus.*, 1888, p. 180.) Finally, Mr. J. A. Allen, in a letter to the writer under date of June 14, 1889, says, "I know of no South American forms near *Chamæa*, outside of the Wrens, of which South America furnishes a large and varied assortment."

With these facts before us, it would seem that a careful comparative study of the structure of *Chamæa* could be nothing less than a well-chosen task, and one decidedly worthy of the labor required to complete it. It is such a work that I have to present in the present paper, and I am indebted to a number of my friends for material wherewith to prosecute it. Chief among these it gives me pleasure to thank Mr. F. Stephens, of Ballena, California, for upwards of a dozen specimens of *Chamæa fasciata henshawii*, and adult and young of *Thryothorus b. spilurus*; this material was collected for me by Mr. Stephens, and generously donated by Mr. G. Frean Morcum, of Chicago. They were all alcoholics. Ten or twelve years ago I also received a good skeleton of *Chamæa fasciata* from Mr. C. A. Allen, of Nicasio, California, and my thanks are due to the same naturalist for a specimen of *Parus rufescens* in alcohol. Mr. Herbert Brown, of Tucson, Arizona, sent me a series of beautiful specimens of *Auriparus flaviceps* and *Campylorhynchus brunneicapillus*, which yielded some excellent skeletons, for which I was especially grateful. My valued friend, Professor Alfred Newton, F.R.S., of Cambridge, England, generously sent me alcoholics of adult ♂ and ♀, and juv. of *Accentor modularis*, which were suggested by him to be compared in the same connection. It was also through Professor Newton's kindness that I obtained from his friend, Lieutenant W. Wilfrid Cordeaux, of the 2d Dragoon Guards (Queen's Bays), some fine alcoholic specimens of the *Paridæ* of the Northwestern Himalayas. Still later I was favored by Dr. George Bird Grinnell with a specimen of *Perisoreus canadensis capitalis*, with which I intended to make some comparisons of the skeleton between it and representatives of the sub-genus

*Lophophanes* among the Titmice. Lieutenant Cordeaux kindly made the collection especially for the present work in the region indicated, and Dr. Leonard Stejneger did me the service of identifying the specimens after they came into my hands. Dr. Grinnell secured the Jay, to which I have just alluded, in Wyoming, and my thanks are due him for his thoughtfulness in the matter. Finally, I am much indebted to Mr. H. K. Coale, of Chicago, for numerous alcoholic specimens of North American Tits and Wrens sent me at different times to be used in the present memoir. My own collection affords either alcoholic specimens or skeletal preparations of an extended variety of our United States *Paridæ*, *Certhiidæ*, *Cinclidæ*, *Troglodytidæ*, and *Mniotiltidæ*, which I have collected during the past fifteen years in widely separated parts of the country.

From the material at hand it will be seen, then, that the principal forms that we lack for comparison are the various species of Wrens of the South American avifauna spoken of by Mr. Allen in his letter, and no one can regret more than the writer the absence for such a purpose of such species as are to be found in the genus *Cinnicerthia*, to which we have already alluded. But as those birds have never as yet been carefully examined and compared structurally with the species to be thus dealt with in this paper, we are just as likely to find them to be Wren-like Tits, a little nearer the Wrens than *Chamæa*, as anything I know anything about. In its topographical characters *Cinnicerthia unirufa*, to be sure, very much resembles *Chamæa fasciata*, indeed very much more so than do either one of them resemble any of our North American Wrens.

Not long ago Mr. Sharpe described a new species of *Cinnicerthia*, in the Catalogue of the British Museum, I think, that looks from the drawing still more Wren-like than the two species alluded to in the previous paragraph, it possessing a longer bill and being still more distinctly barred on the wings and tail. Dr. Sclater in his *Nomenclator Avium Neotropicalium* places the *Cinnicerthia* among the Wrens, and next before the genus *Campylorhynchus*; and a number of ornithologists are of the opinion that our genus *Thryothorus* is the most nearly related genus of Wrens to *Cinnicerthia*, — that is, in the United States avifauna.

Among the typical Tits, so far as I have examined them, we

find no species that particularly resembles *Chamæa* in its general appearance. A mounted specimen of the Bearded Tit, in the collections of the Smithsonian Institution, which was shown me by Mr. Robert Ridgway, has some external characters, both in general form and less so in color, that suggest to our mind an affinity with perhaps some such form as our *Chamæa*. Beyond it, I found no species that appeared to offer any clue.

However, as I said before, if we confine ourselves strictly to the United States avifauna in the comparisons we make with *Chamæa*, I am strongly inclined to believe that in the entirety of its structure it will possess more parine rather than troglodytine characters in its organization. For instance, when we come to consider *all* the external characters of *Chamæa*, its habits, its nest and eggs, its habitat, and other matters bearing upon its history as a species, — taking all these, I say, into careful consideration, and without any regard to its internal structure, and even setting aside for the present its pterylography, I see its nearest allies in the various species of *Psaltriparus*, and secondly, in some very few particulars, in the sub-genus *Lophophanes* among the *Paridæ*. In point of size and in the tufted feathers of the head it more nearly resembles the last-named; while in habit, and in its rounded wings and long, graduated tail, and other points, it comes closer to species in the first-mentioned genus. Its resemblance to such a species as *Auriparus flaviceps* is, of course, very slight, and indeed that somewhat highly colored little bird is the most un-Tit-like-looking Tit that has been allowed a place among our United States *Paridæ*.

In the subjoined TABLE I contrast a few of the characters, etc., which characterize the subject of this memoir and such other species and genera as *Psaltriparus*, *Auriparus flaviceps*, *Parus*, *Accentor*, and *Thryothorus*. When Professor Newton sent me the specimens of *Accentor modularis* to compare with *Chamæa*, he was, I think, more especially impressed with the fact that both the birds laid *blue* eggs, and in both the habits are not altogether unlike. As our examinations into the structure of these forms progress, however, I am convinced that *Accentor* will prove to be a form very much like some of our larger American Warblers, such as for instance *Geothlypis macgillivrayi*, or perhaps some other. I have examined, through the

TABLE.

SPECIES AND GENERA.	GENERAL FORM.	CHARACTER OF PLUMAGE.	PREVAILING COLORS IN PLUMAGE, ETC.	TARSUS AND OTHER POINTS.	NEST, EGGS, AND REMARKS.
<i>Chama fasciata.</i>	Tit-like rather than Wren-like.	Soft and lax.	Various shades of brown.	Obsolutely scutellate; iris white.	Nest in bushes; eggs plain greenish blue (Cones).
<i>Psoltriparus</i> (the genus).	Very small species; Tits.	Soft and lax; tail long as in <i>Chamaa</i> .	Ashy-gray, paler below, not crested.	Distinctly scutellate; iris yellow or brown.	Nest pensile, large, side-opening; eggs 6-9, plain white.
<i>Auriparus flaviceps.</i>	Sylvicoline.	Compact; not especially soft.	Head <i>yellow</i> ; red in wings; general color ashy.	Ditto. Tail short; head not crested.	Nest globular; eggs spotted and white.
<i>Parus</i> (N. Amer. forms of the genus).	Strictly parine.	Loose, long and very soft, may be crested or the reverse.	Black, gray, and white; tail may be long or short.	Distinctly scutellate; iris dark.	Nest excavated; eggs 6-9, white, and spotted.
<i>Accentor modularis.</i>	Sylvicoline chiefly.	Not particularly compact.	Brown; head not crested; tail rather long.	Distinctly scutellate.	Nest in bushes; eggs 6, blue.
<i>Thryothorus</i> (N. Amer. forms of the genus).	Compact; typical Wrens.	Very compact; heads not crested; tail short.	Brown; various shades. Shows markings.	Scutellate. Nostils exposed, not feathered over as in Tits.	Nest built in any suitable nook or receptacle; eggs white and spotted.



courtesy of Mr. Ridgway, skins of both *A. modularis* and *A. vulgaris*, and this recent examination has in no way altered the opinion I expressed on this point a year or more ago; indeed, it has in fact only strengthened it. So far as its topographical anatomy goes, *A. modularis* has all the appearance of a large ground Warbler; still, I intend to carry it along in our examinations in the present monograph, as it will widen the field and prove useful in other ways.

*Of the Pterylography.*—Upon plucking a specimen of *Chamæa*, the ornithotomist is at once struck with the great length of the thighs and legs as compared with the size of the body of the bird. Further, it becomes evident that the pectoral limbs are relatively short, a short brachium, antibrachium, and pinion, and likewise this species has a short, thickset neck. As we would naturally expect, we find the pattern of the pterylographic areas to be passerine, with the “saddle tract” of the spinal pteryla to be rather small and distinctly lozenge-shaped. The continuation of this from its posterior angle to the uropygial (and untufted) gland is composed of almost a single line of feathers. The “ventral tracts” seem to present nothing peculiar.

After removing the plumage of a specimen of *Parus inornatus griseus*, it is seen to markedly differ in form from *Chamæa*, being indeed in contour the perfect miniature of a Jay in this particular; and this species may remotely link the *Paridæ* and the *Corvidæ*, perhaps through such a genus as *Perisoreus*. As to its pterylography, we find the “ventral tracts” considerably broader in proportion than they exist in *Chamæa*, while the “saddle” of the spinal tract is more inclined to be rounded at its corners, though the same meagre line of feathers is continued from it below to the tail. There is a great deal to be learned by the careful study and comparison of the *plucked* bodies of birds, and similarity of form should be given its due weight. I was never more thoroughly impressed with this fact than when I for the first time compared the plucked bodies of a Swift and a Humming-bird. No two birds could be more thoroughly dissimilar than these in this important particular. *Parus inornatus griseus* has the “alar tracts” very densely feathered, and in this species there is an evident tendency for the tracts of the shoulders and neck to run together,—not so, however, in the subject of our paper.

Serving a specimen of *Psaltiriparus plumbeus*, as in the foregoing specimens, we at once recognize how very much it agrees in form with *Chamæa*, and how it differs from *Parus inornatus griseus*. Once more we find the disproportionately long thighs and legs, with the short, thickset neck, though in *Psaltiriparus* the pectoral limbs are relatively larger with respect to the size of the body than they are in *Chamæa*.

The pattern of the several pterylographical tracts are almost identically the same in these two genera.

With respect to form and pterylography the Chickadees, as represented by *Parus gambeli*, seem to offer the precise intermediates between *Chamæa* and *P. i. griseus* (*Lophophanes*), or between *Psaltiriparus* and the latter. For in them we find a harmonious balance between limbs and body, though the pelvic pair are rather long. The neck is proportionately longer, and the head moderately smaller. Indeed, one might say in the body of this Chickadee there are really no proportional discrepancies, any more than there are in the form of the body in an average Sparrow. This mountain Chickadee likewise shows some departure in its pterylography, for the ventral tracts are much narrowed; the saddle of the spinal tract lozenge-shaped again, while quite a broad band of feathers, several rows at least, connect this latter with the dorsal caudal pteryla. All the Tits I have thus far plucked have the skin of the head, with the exception of that covering the throat, of a dark purplish hue; and I am inclined to think that this is normal with them.

At some other time the writer has it in his mind to give the anatomy of the genus *Sitta*; and as there can be no very intimate affinity between it and *Chamæa*, we will not take it into consideration here. This should not debar us from taking a glance at such a form as *Regulus satrapa*, and I am under obligations to Mr. H. K. Coale of Chicago for alcoholic specimens of this species. After one has been carefully plucked its diminutive body calls up to us *Psaltiriparus*, but not so its form; for in *Regulus* we have the true sylvicoline contour, with its far more *acutely* conical head, the deep-set eyes, the justly proportioned limbs for the size of the body, which latter is robust, broad, showing evidences in front of the more prominent keel of the sternum.

*Regulus* has a large, lozenge-shaped saddle in its spinal tract;

and this pteryla is quite broad, as it is continued on to the tail, the whole system of the pterylography causing the feathering to be quite dense in this species.

Both the form of the body and its pterylography in *Regulus* is substantially repeated in *Polioptila plumbea*, a specimen of which species I have this moment plucked, and now have before me. In it, however, there is an evident arrangement of the feathers in the capital area; for a strong, single, median row can be easily recognized, and another single row passes over each eye. The median row bifurcates anteriorly, the base of the culmen passing between the limbs, which latter have on either side the lateral orbital row merging into it. Judging from form of body and pterylography alone, I would hardly say there was any very close affinity between *Chamaea* and the last two genera we have examined.

In the lot of alcoholics kindly collected for me by Mr. Coale, I also find an excellent specimen of *Certhia familiaris americana*; but aside from its curved and slender beak, the form of the body of this species is sylvicoline, with troglodytine affinities quite pronounced, while its pterylography is strictly passerine. From its topographical anatomy, and what we know of its habits, it surely has but a very slender kinship with *Chamaea*.

The pterylography of *Certhia familiaris* has been correctly figured by Nitzsch.<sup>1</sup>

Passing next to one of our specimens of *Accentor modularis*, I find upon plucking it that its pterylography is very different from *Chamaea*, having quite the same pattern which Nitzsch figures for *Motacilla alba*,<sup>2</sup> though in *Accentor* the saddle tract of the dorsum is if anything proportionately larger, and the pteryla leading from it to the uropygial gland broad, and spreading posteriorly at its termination. All the pterylæ are clearly defined and strong in the *Accentor*.

The form of the body in this bird is what one might suppose to be as a cross between one of our average Sparrows and a large Warbler, say for instance, *D. vigorsii*  $\times$  *Ammodromus*, at once noticeably different in contour from the subject of our paper. An arrangement of the feathers on the top of the head in this species are as I described them for *Polioptila*, with the exception

<sup>1</sup> *Pterylography*, Eng. ed. by Slater, Taf. III., fig. 3.

<sup>2</sup> *Ibid.*, Taf. III., figs. 1 and 2.

that the median band is much broader. And I wish it to be understood that in both species scattered feathers are to be found interspersed among the three longitudinal bands which I have attempted to describe. This condition is also pretty well seen in *Chamæa*. There is but one other species we will examine just at present, so far as its topographical anatomy goes; and I propose to allow *Salpinctes obsoletus* to represent the Wrens, it being a good-sized Western form. In it we find a pterylography which approaches *Certhia* more nearly than any other species we have investigated, while in the form of its plucked body, it widely departs from *Chamæa*, as its head is conspicuously large for its size; the neck rather long; the body or trunk very wide and compressed dorso-ventrally; the pectoral limbs long and powerfully developed; and finally, the pelvic extremities relatively short, and not especially strong. *Chamæa fasciata* has very little affinity with this bird, so far as is indicated by external features and characters; and these are as much a part of its anatomy as are brain, viscera, or skull. The form of the plucked body in *Salpinctes obsoletus* is substantially repeated in *Campylorhynchus brunneicapillus*.

To sum up a little, then, as far as we have gone, and spreading out before us all our specimens of plucked birds now under consideration, carefully reweighing everything that has been set forth in the foregoing paragraphs, — then by a system of elimination, putting first aside the species having the greatest number of different characters, then the next one most evidently unlike our *Chamæa*, we find at last that we are compelled to decide in favor of a *Psaltriparus* as having the majority of characters in its external parts that approach the subject of our present memoir.

Turning for the moment to such foreign forms as *Ægithaliscus erythrocephalus*, *Parus nepalensis*, and *Parus xanthogenys* from the northwestern Himalayas, we find some interesting comparative points in them; for in the first-named species the general form of the plucked bird quite nearly resembles *Chamæa* and the Bush-Tits of the genus *Psaltriparus*, in that its pterylography is very much the same; while the shape of the head, the shortish neck, and the lengthening of the pelvic limbs, though the latter is not so striking, all point to a parine structure, which approaches our Wren-Tit.



This, however, does not apply to the two last-mentioned species, for in them these characters are far more like what we find in some of our typical Titmice, more especially such species as *Parus gambeli* or *Parus atricapillus* and its varieties.

I would also especially note that the shape of the bill in *Æ. erythrocephalus* more nearly approaches that part of the anatomy in *Chamæa* than any other bird which I have compared with it, or which is supposed to bear any relationship with it. Let us next cut down upon some of the internal structures, and see what they seem to point to, in the way of affinities.

*The lower larynx or syrinx* in *Chamæa*, both in structure and its musculature, seems to depart in no way whatever from its constitution in the smaller passerine birds generally. I have examined it in a number of species, including *Accentor* and the *Paridæ*.

The *tongue*, agreeing in its principal features with the tongue in true passerine birds, has, nevertheless, its extremity in *Chamæa* bluntly truncated square across, and this margin finished off with a fringe of fine fimbriations. This is the case in most of the Tits, while in the Wrens (*Salpinctes*) the extremity of the tongue seems to be simply pointed, and in *Accentor* it is distinctly once notched in the middle line, with the bifurcations showing a tendency to fringe.

As usual in Passeres the left carotid artery is the only one present, not only in our subject, but in all others examined.

Upon examining the *intestinal tract*, we find the pair of small cæca present in all the species under consideration, and *Chamæa* agrees with both Wrens and Tits in possessing a wonderfully small gizzard. And in these birds the organ consists of a strong, firm internal corneous coat, overlaid by a thin and delicate muscular one which readily peels off, leaving the complete corrugated cast of the dense internal layer. This is the case also in the Himalayan Tits referred to above. *Accentor modularis*, on the other hand, has a conspicuously large gizzard of very different structure; for although it has a small corneous internal coat, this latter is covered by a thick and strong muscular layer, and upon opening it I find numerous pieces of hard, flinty gravel (as large as No. 8 shot) mixed with seeds and insects. Measuring the greatest median longitudinal line of the plucked head of a specimen of *Chamæa*, we find it to be equal

to 3.2 cms., while the greatest diameter of its stomach in any direction is equal to 1.2 cms. Now the same measurements for the following species are:—

	Head	Stomach
<i>Parus inornatus griseus</i> . . . . .	3.2 cms.	1.1 cms.
<i>Accentor modularis</i> . . . . .	3.1 “	1.7 “
<i>Salpinctes obsoletus</i> . . . . .	3.9 “	1.3 “
<i>Psaltiriparus plumbeus</i> . . . . .	1.9 “	0.9 “

Further, I would add that the corneous layer of the gizzard in *Accentor* is much thinner than we find it in the Wrens and Tits, while the external form of the organ is entirely different.

Having carefully examined the myology of the limbs in *Chamæa* and compared it with the corresponding structures in Tits, Wrens, Warblers, and the *Accentor* and others supposed to be more or less nearly related to our subject, I find no essential differences that will aid us in determining affinities. In all these forms, so far as I have been enabled to discover, the origin and insertion of the patagial muscles of the arm and the thigh muscles are essentially passerine.

With these investigations of the “soft parts” of *Chamæa* and its supposed affines before us, we will next pass to a comparative consideration of its skeleton.

#### OF THE OSTEOLOGY.

*The Skull.*—A great many of our smaller and ordinary passerine birds, such as the Wrens, Warblers, and some few others, have the superior osseous mandible, and the large subelliptical narial aperture on either side of it, constructed very much upon the same plan. The culmen is more or less curved gradually from frontal region to apex; the lateral edges are cultrate; and there is never any bony *septum nasi*, while it is entirely open on the under side between the delicate anterior limbs of the palatines. Seen upon side view, this pattern of the upper bony beak is well shown in *Chamæa* or in *Psaltiriparus* or in *Regulus* (Figs. 1, 3, and 4), while, though the plan remains identically the same, the form is somewhat altered by the lengthening of the beak in such Wrens as *Salpinctes* (Fig. 7), *Thyrothorus b. spilurus*, and the Cañon Wren (*Catherpes*). It is seen again in the Warblers, where recognizable differences of form obtain to an extent in this part of the skull sufficient to

allow us to distinguish between the genera in some cases — not always an easy matter. For instance, in the numerous skulls of Warblers before me, the superior osseous mandible of *Dendræca æstiva* is markedly more like *Chamæa* in this particular than is the Prothonotary (*Protonotaria*), and *Mniotilta* more than either.

In this particular *Psaltriparus plumbeus* (Fig. 3) is most like *Chamæa*; *Accentor* agrees better with some of our *Mniotiltidæ*; while a departure becomes evident as we pass to certain Titmice.



fig. 1.



fig. 2.



fig. 3.



fig. 4.



fig. 5.

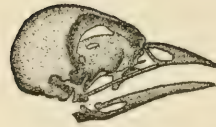


fig. 6.



fig. 7.



fig. 8.

Figure 1. — *Chamæa fasciata*.

Figure 2. — *Accentor modularis*.

Figure 3. — *Psaltriparus plumbeus*.

Figure 4. — *Regulus satrapa*.

Figure 5. — *Parus* [*Lophophanes*] *inornatus griseus*.

Figure 6. — *Parus gambeli*.

Figure 7. — *Salpinctes obsoletus*.

Figure 8. — *Certhia familiaris americana*.

These figures are all right lateral views, and life size, by the author, from the specimens.

This change begins to be apparent in the Chickadees, as in *Parus gambeli*, or in the skull of *P. carolinensis* of a specimen kindly presented me by Mr. Coale, or in *P. rufescens*. It consists mainly in a decrease in the size of the openings of the nostrils, and a broadening of the culmenar bridge between them. And it is in such species as *Parus inornatus* (of the subgenus *Lophophanes*) that we find a vastly different state of affairs prevailing (Fig. 5), for in them the upper bony beak is shorter; less pointed anteriorly; broadly rounded from side to side for the entire length of the culmen; the narial apertures subcircular instead of subelliptical in outline; their superior arcs widely separated by the great width of the nasal processes of the premaxillary. Viewing the skull upon its superior aspect, we find that in *Chamæa* the frontal region is extremely narrow between the upper edges of the orbits, more so, in comparison with its size, than in any other species we have under consideration, although the feature is common to them all. The cranial vault, the sides and back of the brain-case included, is a smooth and rounded dome in *Chamæa*, the Wrens, Tits, *Accentor*, *Regulus*, and the rest, though it differs in the various genera and species, both in form and relative extent. For the size of the bird, *Chamæa* has decidedly the largest cranial capacity, *Psaltriparus* about equalling it in proportion to its size, followed by *Parus inornatus*, then *Regulus* and the Chickadees; while the Wrens have a small brain-case as compared with their size, the same applying to *Accentor* and our Warblers. *Lophophanes* has the posterior moiety of either orbital rim raised all round, a feature less marked in the Chickadees, while in *Chamæa*, the Bush-Tits, and Wrens it does not exist.

Some good distinguishing characters are also to be found on a lateral aspect of the skull, more especially in the condition of the interorbital septum. Barely any bone is to be found here at all in *Chamæa*, it being absorbed by a large vacuity occupying the central part of the partition, separated only by a slender bar from the great coalesced openings above where issue the first pair of nerves. The optic foramina have also merged, and it consists now in a small, central, circular foramen completely surrounded by bone, at the median point of the upper arc of which the posterior end of the extremely delicate osseous rod which bounds the interorbital vacuity above is attached. *Psal-*



*triparus* and most Wrens repeat this state of affairs almost exactly (compare Figs. 1, 3, and 7), while the septum is more nearly complete in *Accentor*, while in the Tits, more especially in *Lophophanes*, it comes very near being entirely so (Figs. 5 and 6). The zygoma is reduced to almost hair-like dimensions in all of these species, and the *pars plana* separating the orbital and rhinal spaces is comparatively large, tumorous, and of a quadrilateral form. Few characters, if any, are afforded by the posterior aspect of these skulls; in all this part of the cranium is rounded, quite smooth, always shows a supraoccipital prominence, but never the foramina on either side of it. So well known is the arrangement of the palatal osseous structures at the base of the skull in these ordinary passerines, that we will refrain from entering upon a detailed description of them here. The various parts, more particularly the palatines and maxillo-palatines, differ to some extent in form in the several genera and species, but the arrangement remains essentially always the same. In all except *Lophophanes* the vomer is truncated anteriorly and variously notched, while in the excepted genus this bone shows a longitudinal median carination beneath, and is carried, in the specimen before me, to a point in front, as a whole it being shaped something like a diminutive oblanceolate leaf. *Psaltriparus plumbeus* has the bony structures at the base of the skull most like the corresponding ones in *Chamæa*; the Wrens and Chickadees seem to stand next in this regard, *Accentor* approaching the *Mniotiltidæ*. Generally the narial ends of the maxillo-palatines are dilated into a small paddle-shaped extremity, but in such a form as *Regulus satrapa*, however, no such enlargement exists, these processes each being long and very slender. Normally, they are not in contact either with each other or with any of the surrounding bones, and the vomer fuses with the palatines behind.

Of no very great strength in any of the species before me, the *mandible* in all is of a V-shape form, and differs principally in the size of the ramal vacuity. This is very large, relatively, in *Chamæa*, *Psaltriparus*, Crested Tits, Chickadees, and some others, but notably diminished in size in most Wrens, where it may disappear altogether in some species.

Nothing worthy of special note characterizes the hyoidean apparatus, still less the intrinsic ossifications of either the eye or

ear, their structure in these passerine types being well known, as is the fact that they seldom, if ever, offer us any important characters upon which to assist us in determining affinities.

*Of the Remainder of the Axial Skeleton.* — There are nineteen free vertebræ between the skull and the pelvis in the spinal column of *Chamæa fasciata*, and of these the first eleven are without ribs; the twelfth supports an exceedingly minute pair of rudimentary riblets; on the thirteenth these are longer; on the fourteenth they are fully developed, and have uncinæ processes, but do not reach the sternum. The next five vertebræ bear complete ribs, which connect with the sternum by hæmapophyses, and the thoracic ones all have long slender uncinæ processes; finally, there is a pair of "sacral ribs," without these latter, and whose hæmapophyses fail to reach the costal border on either side of the sternum.

*Psaltiriparus plumbeus* agrees thus far, with respect to the vertebræ and ribs between skull and pelvis, with *Chamæa*, and in both species the ribs in particular are very delicate structures; in the Bush-Tit being fully as much so as the ribs in a skeleton of the Rivoli Humming-bird (*Eugenes fulgens*), for which I am indebted to Mr. W. W. Price, of Tombstone, Arizona, who recently collected the specimen near that place, and presented it to me.

We also find, in this part of the spinal column, nineteen vertebræ in *Accentor*, but this species differs in this, that the hæmapophyses of the last dorsal vertebræ do not arrive at the costal borders of the sternum. This arrangement disagrees even with our North American Warblers (*Compsothlypis*, *Dendroica*, *Protonotaria*, and several others), and just at this moment I fail to recall to mind the sternum of any ordinary small passerine bird, that has, as have the two sterna of *Accentor modularis* before me, but *four* hæmapophysial facets upon either costal border. I pointed out several years ago that in *Otocoris* the first pair, or one of the first pair, on either side, of the hæmapophyses, may fail to be present, and thus have a sternum with only four facets on either border, but in *Accentor* the missing facet is at the other end of the row. (*Contributions to the Anatomy of Birds: Osteology of Eremophila.*)

The ultimate hæmapophyses in *Accentor* barely clear the costal borders of the sternum, and it is just possible that speci-

mens may be found wherein their lower ends make their impress on the lateral sternal margins.

In a specimen of Parkman's Wren, which I collected here at Fort Wingate, New Mexico, in 1885, there are also nineteen vertebræ in the column, between skull and pelvis, with the same arrangement of the ribs as in *Chamæa*, but the twelfth vertebra, although the vertebral canal on either side of it is not closed, its pleurapophyses have not either been liberated as a pair of tiny ribs. This may prove to be the case in the majority of specimens of *Chamæa*, but it is a matter of minor importance.

Among the Titmice (*Parus*) the same arrangement of the vertebræ and their ribs obtains in this, the cervico-dorsal division of the column, and I am inclined to believe it to be characteristic of the majority of groups of oscine birds; *Sturnella*, the Orioles, and some of the Crow-Blackbirds forming the principal exceptions. (See author's "The Skeleton in the Genus *Sturnella*," etc., *Journal of Anatomy*, London, April, 1888, Vol. XXII.) The comparison of this part of the skeleton then, in *Chamæa* and its supposed affines, will not assist us much as a diagnosis of possible kinships among the various species under consideration, so we will next take a look at the pelvis.

*Chamæa* has a pelvis fashioned after the general passerine type or model, and its sacrum, or the number of vertebræ that have co-ossified with it, seem to be twelve. This part is very large, as may be seen by examining it upon its ventral aspect, where a longitudinally disposed parial row of quadrilateral pit-lets mark it for nearly its entire length. The obturator space is very large, while the hinder ends of the post-pubis and ischium on either side flare outwards a good deal. Proportionately, the ischiadic foramen is also big, and the obturator foramen completely surrounded by bone. Viewing this pelvis from above, we note that the præacetabular portion is narrow, and the ilia much concaved, the fore part of the internal margins of these bones not meeting here, but they gradually approach each other, and are finally in contact in the middle line, at a point just a little anterior to an imaginary line joining the acetabulæ. The post-acetabular space is broad, and of a quadrilateral outline. More or fewer pairs of interdiapophysial foramina are here seen, disposed as usual in a double row.

Of all the pelves before me, none approach, in detail, this pel-

vis of *Chamæa*, so closely as does the pelvis of *Psaltriparus plumbeus*, in which species this bone is quite the miniature of our subject's. One point, however, must be noted, and in the *Psaltriparus* the ilia do not come quite in contact on the dorsal aspect, as we have stated above to be the case in *Chamæa*.

Passing to the Crested Tits (*Lophophanes*), the pelvis still bears the same general features, but in it the internal margins of the ilia, opposite the acetabulæ, are yet further separated, and the sacrum here upon the dorsal aspect thoroughly exposed, in consequence, for its entire length.

Chickadees and Wrens are in the same case, their pelves agreeing very well with the others described, and with the sacrum well in sight along its entire dorsal aspect, the ilia not meeting each other in any part of that locality.

*Accentor* has a very different pelvis from this; and it agrees best with that bone in some of our larger *Mniotiltidæ*, with a trace of the Sparrow in it, and belongs to a bird quite thoroughly removed from *Chamæa*.

Counting the free *caudal vertebræ* in our subject, I find there are *six* of them, not including the large *pygostyle*. This latter bone has here rather a peculiar shape, its superior laminar portion showing near its centre an area where the bone is much thinner than at the edges; while below it is somewhat spread out, after the fashion of the *Pici*, only in a far less degree.

Six plus a *pygostyle* is also the normal complement in *Psaltriparus* and all other Tits examined, as well as in the Wrens, and in *Accentor*, and finally in such species as *Polioptila plumbea*, *Regulus*, and *Protonotaria citrea*. Let us next take a glance at the bones of the *shoulder girdle* in these several groups of birds; and first, in *Chamæa*, we find the *os furcula* to assume the broad and deep U-shape pattern, its limbs being reduced to almost capillary dimensions, with a mere apology below for a hypocleidium, while the coracoidal ends of the limbs are comparatively very much expanded. A *scapula* has a long, narrow, thin blade, the posterior third of which is turned considerably outwards, and its apex carried to a fine point. Most interesting, however, of all three is a *coracoid*, which here attains to a wonderful length, the bone being not a little longer than the greatest longitudinal diameter of the body of the sternum (not including the manubrium in the measurement). Its shaft is subcylindrical



and straight, with its sternal end only moderately expanded, as is the other extremity of the bone, only moderately tuberos. When articulated *in situ*, these bones show no marked departures from the corresponding arrangement in all ordinary oscines. The Bush-Tits (*Psaltiriparus*) have the bones of the shoulder girdle in all respects very similar to those just described for *Chamæa*, not omitting the unusual length of the coracoids, which here lack but little of being fully as long as the entire sternum.

In *Lophophanes* the hypocleidium of the os furcula is inclined to be slightly more prominent; but beyond this minor difference, little change is to be discovered in the elements of this pectoral arch, beyond what has been given above.

*Troglodytes* among the Wrens may have the furcular hypocleidium still more conspicuous, and this also applies to the genus *Salpinctes*. Os furcula among these latter birds still retains its frail structure, a broad U in form, gently curved backwards for its inferior moiety, which curvature begins almost imperceptibly near its middle.

When we get among the skeletons of the Warblers (*Mniotiltidæ*), little change is to be found in the shoulder girdle; but with them the hypocleidium of the fourchette is always of good size, as it is in *Accentor modularis*.

*Chamæa fasciata* has a *sternum* of the well-known passerine pattern. It is peculiar, however, in that it is strikingly flat, there being but little concavity apparent upon its thoracic aspect. Its outer xiphoidal processes are wonderfully slender, and the midportion very broad behind, which latter fact renders the outline of the body quite square. Its keel is shallow and weak. Indeed, the entire bone in this bird is a very delicate one, as compared with the size of its owner. *Psaltiriparus plumbeus* has a sternum the very counterpart of the bone in *Chamæa*, only in miniature. Its body, however, is more concaved, and the mid-xiphoidal margin not so long comparatively. Its pattern is considerably changed in the Crested Tits (*Lophophanes*), where the body is far more oblong rather than square; the mid-xiphoidal margin much more contracted; the "notching," comparatively speaking, not so profound as in the Bush-Tits; the keel more ample; and the costal processes and manubrium strongly developed. The latter shows a deep carination beneath, which is scarcely at all evident in *Chamæa*. *Troglodytinæ*,

although they have, as a rule, a sternum in each species with a style to it of their own, yet by the slightest modification it could be easily made to assume the pattern of the bone, as we find it among most North American *Parinæ*. For example, how much the bone is alike in two such species as *Salpinctes obsoletus* and *Parus inornatus* ! Again, take three such sterna as are offered us in the skeletons of *Protonotaria citrea*, *Accentor modularis*, and *Icteria virens*, and how marvellously close is the similarity, even to the most insignificant details (barring the one less facet on either costal border, in the case of the second-named species) ; and if guided alone by their form, how difficult it would be to distinguish them without any other assistance ! And yet, were the sternum of *Psaltriparus plumbeus* brought up to the size of the sternum in the Prothonotary Warbler, we would have no difficulty in such a matter, notwithstanding the fact that the general pattern in both is the same ; and how extraordinary is the gentle gradation in form between two such species, in this part of their skeletons, with respect to species of intermediate affinity !

*On the Appendicular Skeleton : the Pectoral Limb.* — As is usually the case, the several bones of the limbs of these small passerine birds offer us but a slender list of distinguishing characters, in any way pointing to the affinities of the species compared. In *Chamæa* the bones of both extremities appear to be completely non-pneumatic, whereas in such a Tit as the *Parus inornatus* both the humerus and femur have air admitted to their shafts ; and I am not certain but that the long bones of the antibrachium and leg are in the same case. Other Tits also have the arm and thigh bones pneumatic. The *humerus* in our subject is characterized by having a notably straight shaft, and for its brevity, as compared with the size of its owner. Its head and distal extremity, however, are in harmonious proportion with its length ; while the small glenoid cavity of the shoulder girdle, intended for its articulation, is re-inforced by a fair-sized *os humero scapulare*, in which it agrees with other species and genera before me.

Both bones of the antibrachium, the *radius* and *ulna*, are likewise very short and very straight. This may be best appreciated by stating the fact that the radius in *Psaltriparus plumbeus* comes within a hair's breadth of being fully as long as that bone

in the forearm of *Chamæa*, yet see the difference in the size of the skulls of these two birds in Figures 1 and 3. Another way we have of contrasting such a matter is by the fact that the tibio-tarsus in *Chamæa* is very nearly three times the length of its radius, and the tarso-metatarsus is nearly double its length. Nothing specially noteworthy is met with in the skeleton of the pinion in our subject. Measured from the head of the carpo-metacarpus to tip of the most distal phalanx, this division of the skeleton of the pectoral limb is nearly as long as the ulna. The Bush-Tits have these parts quite in proportion with the size of their bodies, but otherwise the form of the bones is pretty much the same.

*Parus inornatus* (*Lophophanes*) presents some peculiarities in the skeleton of its antibrachium and pinion, for the outer surface of the proximal third of the shaft of the radius always develops a scale-like projecting ledge. While the proximal phalanx of the index digit is flat and smooth upon its radial side, it is deeply excavated for the entire length of its anconal aspect; and finally, the slender middle digit extends for an unusual distance below the main shaft of the carpo-metacarpus (or index digit), allowing its rather large and single phalanx to descend to a point considerably below the middle of the hinder margin of the proximal phalangeal joint of the index finger, whereas, as we know, in most birds it is stowed away in the recess at the upper third of this joint. *Chamæa* also reveals its parine affinities in this particular, for the skeleton of its pinion is constituted pretty much on the same plan.

Wrens have their arm-bones a good deal like we find them in the *Parinæ*, but here a noticeable flattening of the radius always seems to be present, and characterizing the proximal moiety of the shaft of the bone.

*Accentor modularis* offers us nothing peculiar in its skeletal wing structure worthy of especial note; it is formed upon a strictly passerine type.

*The Pelvic Limb.*—So far as the characters of the bones of this limb themselves are concerned, they present so few strong differential ones to assist us in determining affinities that we might with great propriety pass them by at this point, but still a word in regard to other matters concerning them will not be out of place. In *Chamæa* all the long bones of the pelvic limb

are conspicuous for their slenderness, and in the case of the tibio-tarsus and tarso-metatarsus, for their unusual length; the *femur* in this species is relatively very short, and is convexed forwards near its middle. To show some of these discrepancies in length we have but to present a few measurements:—

TABLE.  
(Metric Measure.)

SPECIES.	LENGTH OF SKULL.	FEMUR.	TIBIO-TARSUS.	TARSO-META-TARSUS.
<i>Chamæa fasciata</i> . . . . .	3.1 cms.	1.6 cms.	3.3 cms.	2.5 cms.
<i>Parus inornatus griseus</i> . . .	3.1 “	1.7 “	2.8 “	2.1 “
<i>Salpinctes obsoletus</i> . . . . .	3.8 “	1.7 “	2.7 “	1.9 “
<i>Psaltiriparus plumbeus</i> . . . .	1.8 “	1.1 “	2.1 “	1.5 “

As in the vast majority of all true oscines,—indeed I cannot recall an exception to the rule,—*Chamæa* possesses a small patella at the front of its knee-joint embedded in the usual tendon. With respect to the *tibio-tarsus*, its cnemial crest is seen to rise well above the articular surface of the summit of the bone; and both its pro- and ectocnemial processes are well-developed. Distally the condyles are very prominent anteriorly, their outer peripheries being nearly exactly alike in outline, and of a uniform shape.

The shaft of this bone is wonderfully straight and of nearly the same calibre from one end to the other. Its associate in the leg, the *fibula*, is of very diminutive proportions, freely attached, and ossifies for only a short distance below its ridge for articulation on the shaft of the tibio-tarsus. *Tarso-metatarsus* also has a straight shaft, for the most part flattened in front and rather sharpened behind. The hypotarsus is comparatively prominent, and shows both grooves and canals perforated for the passage of tendons. At its extremity, the mid-trochlea is seen to be situated the lowest upon the shaft, and all three of these projections are very much in the same plane, or the one, approximately speaking, in which the anterior flat surface of the shaft may be said to lie.



The "accessory metatarsal" is comparatively large as compared with the associated parts and supports a strong basal joint for the hallux digit. This is also the case in *Salpinctes*, another species which spends much of its time on the ground.

The arrangement of the joints of the toes, 2, 3, 4, and 5, for hallux to fourth toe respectively, is strictly passerine and presents nothing worthy of especial remark.

Aside from what I have pointed out then in the last few paragraphs touching upon the pelvic limb, the ornithotomist may be well assured that no vantage is to be gained, so far as the elucidation of affinities go, by entering upon a detailed comparison of the several characteristics presented in these bones of the supposed affines of *Chamæa*, for such characters are not of a nature of sufficient import to be brought into the discussion with any telling results, and the attempt to utilize such other insignificant differences as I have intentionally passed over, would simply be a profitless task.

In passing, I would say here that I have carefully compared in the present connection the skeleton in *Lophophanes* with a skeleton of *Perisoreus c. capitalis*, and find the latter to be essentially a garruline bird in so far as its osteology goes, and very easily distinguished from any Tit in our avifauna. It was Coues who said of our *Paridæ* that, "really they are hard to distinguish, technically, from Jays; but all our Jays are much over seven inches long."<sup>1</sup> The resemblance, aside from the question of size, and to a lesser extent, of color, in the case of *Perisoreus* and *Lophophanes*, is brought to mind by the agreement in the case of the corresponding morphological details exemplified by the majority of the external characters. It is immediately dispelled by a comparison of the skeleton in the two genera in question; though there may, however, be some remote affinity here.

In that *Chamæa* lays *plain greenish blue* eggs, of course means something; especially as all our Wrens and Tits, as a rule, lay *white* eggs that are more or less *spotted*. Such a single character, however, often persists in a species, being carried down from the original ancestral stock, and to it no unjust weight must be attached. Then, too, it must be remembered that *Chamæa* being related to the Wrens, and these latter surely

<sup>1</sup> *Key to North American Birds*, 2d ed., p. 263.





TABLE.

SPECIES.	GENERAL FORM OF THE SKULL.	EXTERNAL NARIAL APERTURE OF SKULL.	INTERORBITAL SEPTUM.	VOMER.	PALATINES.	MAXILLO-PALATINES.	MANDIBLE.	SHOULDER-GIRDLE.	STERNUM.	PELVIS.	REMARKS.
1. <i>Chamaea fasciata</i> .	Brain-case ample for size of bird; not markedly vertically compressed. Skull somewhat acutely produced anteriorly, and superior mandible slightly decurved.	Each rather a large, longitudinal placed, sub-elliptical opening.	Shows a large central vacuity, and another similar opening above.	Swelled anteriorly where it is <i>truncated</i> and mesially notched.	Rounded postero-external angles; anterior limbs very slender.	Each mesial end rather large, flat, thin, and squarish. Not in contact with vomer.	Moderate V in outline; rather feeble; a fair-sized, elliptical ramal vacuity. The base slightly decurved.	Coracoids long and slender, shafts straight and subcylindrical. Scapulae curved outwards posteriorly. Hypocleidum of U-furcula small.	Two-notched; sub-oblong in outline; shallow carina, lofty costal processes; large bifurcated manubrium.	Iliia meet over sacral crista; a double parietal row of pits down ventral surface of sacrum.	Has the habit of occasionally carrying tail erect like a Wren (Gambel); inhabits "shrubby and weedy places, is restless and active, expert in eluding observation, and clamorous in resenting intrusion of its haunts, with harsh, scolding notes" (Coues). External characters are given in another Table ( <i>antea</i> ).
2. <i>Psaltiriparus plumbeus</i> .	Brain-case = ditto. Skull less acutely produced anteriorly as compared with <i>Chamaea</i> ; superior mandible only slightly decurved.	ditto.	ditto.	Much the same.	Postero-external angles inclined to be more squarish, otherwise ditto.	Quite similar; mesial paddles comparatively thicker.	ditto.	ditto.	ditto; carina proportionally somewhat deeper.	Iliia very nearly meet over sacral crista; otherwise ditto.	Gregarious at certain seasons. Nearly all Timnize have a scolding note whenwile they greet intruders who chance near their nests, or in many cases, even their haunts.
3. <i>Campylorhynchus brunneicapillus</i> .	Brain-case less ample as compared with <i>Chamaea</i> ; somewhat vertically compressed. Skull proportionately very much more produced anteriorly than in <i>Chamaea</i> . Superior mandible decurved.	ditto.	ditto.	More uniform in calibre throughout. Only a shallow rounded notch in front.	Somewhat produced and pointed postero-external angles. Anterior limbs slender.	Mesial ends narrow and longitudinally produced. Quite different from <i>Chamaea</i> .	Acute V in outline; rather strong, and decurved. Ramal vacuity <i>absent</i> .	Coracoid proportionately very much shorter, others nearly ditto for the remaining bones of the arch.	Proportionately more oblong than in <i>Chamaea</i> ; otherwise ditto.	ditto; sacral row of pits nearly <i>obsolete</i> .	A large Wren, approaching <i>Harporhynchus</i> in its structure.
4. <i>Auriparus flaviceps</i> .	Brain-case ample for size of bird; not vertically compressed. Facial portion short and acute. Superior mandible slightly decurved.	Each <i>subcircular</i> in outline. Very different from <i>Chamaea</i> or the Bush-Tits.	ditto.	Vertically compressed; enlarged anteriorly and unnotched.	Postero-external angles produced as <i>long, sharp</i> spines.	Much as in <i>Chamaea</i> .	V-shaped; subcircular ramal vacuity present; angular processes <i>markedly</i> produced behind.	Coracoids not strictly parine. Scapulae rather smartly bent at posterior thirds; hypocleidum comparatively larger.	ditto to last, but its keel comparatively much deeper than in <i>Chamaea</i> .	Iliia well separated from sacral crista. Pits of sacrum beneath, scarcely perceptible.	A Tit, nearest related to <i>Psaltiriparus</i> among our United States <i>Paridae</i> , but with much in its structure connecting it with the genus <i>Comptolophus</i> among the <i>Mniotiltidae</i> . Almost a form that stands between the two families referred to.
5. <i>Catherpes m. conspersus</i> .	Brain-case ample, and <i>markedly</i> compressed in vertical direction. Skull much produced anteriorly; superior mandible slightly decurved.	Each a long, narrow subellipse in outline.	ditto.	Much as in the typical Wrens generally.	Postero-external angles <i>not</i> produced, though angulate. Anterior limbs <i>long</i> and slender.	As in <i>Campylorhynchus</i> .	<i>Acute</i> V-formed; decurved; feeble, and ramal vacuity exceeding minute.	Bones all strikingly slender; scapulae short and <i>dent</i> at ends; hypocleidum of furcula minute.	Square in outline; carina shallow, and withal the bone flatter than in <i>Chamaea</i> .	Iliia do not meet sacral crista. Pits on sacrum nearly obsolete.	A peculiar species of Wren, having a skeleton wherein the skull by its <i>flatness</i> at once distinguishes it from other genera of Wrens in our United States avifauna.
6. <i>Parus i. griseus</i> ( <i>Lophophanes</i> ).	Brain-case rather large, and semiglobular in form. Face of skull short; superior osseous mandible in no ways decurved.	Each <i>subcircular</i> in outline.	With notably small vacuities in it.	Narrow-leaf-shaped, and so <i>pointed</i> in front.	<i>Short</i> ; postero-external angles truncate. Anterior limbs comparatively stouter.	Mesial ends <i>large</i> , squarish, thin, and flat; not touching vomer.	Strong; a V in form; large subelliptical ramal vacuities.	Short, slender coracoid; scapulae narrow, with <i>cn's</i> curved outward; hypocleidum rather large.	Oblong; comparatively deep carina; large, broad costal processes.	Iliia rather widely separated from sacral crista; rows of sacral pits distinct.	Tits which are osteologically quite distinct from any other genus of the <i>Paridae</i> of the United States, and equally so from <i>Chamaea</i> .
7. <i>Troglodytes a. parkmanii</i> .	Brain-case rather small comparatively; slightly compressed. Skull produced anteriorly. Superior osseous mandible decurved.	Each a large, longitudinally placed, subelliptical opening.	As in <i>Campylorhynchus</i> .	Appears to be <i>doubly</i> notched in front, otherwise as in typical Wrens.	As in <i>Campylorhynchus</i> .	As in <i>Campylorhynchus</i> .	Rather feeble; a V-shaped one with a <i>small</i> elliptical ramal vacuity.	Like the typical Wrens, and with the hypocleidum of furcula larger.	Suboblong in outline; carina of moderate depth. Processes all well developed.	Iliia <i>well separated</i> from sacral crista. Pits beneath sacrum very marked.	A typical troglodytine species.
8. <i>Salpinctes obsoletus</i> .	ditto.	ditto.	ditto.	ditto.	ditto.	ditto.	Ramal vacuity absent.	ditto.	ditto.	ditto.	Osteologically, this Wren is nearer <i>Catherpes</i> in its affinity than it is <i>Campylorhynchus</i> .
9. <i>Agithaliscus erythrocephalus</i> .	Brain-case fairly ample; slightly compressed vertically; moderately produced anteriorly; superior mandible slightly decurved.	Each rather large, subelliptical.	As in <i>Chamaea</i> .	Much as in <i>Psaltiriparus</i> .	As in <i>Psaltiriparus</i> .	Each free mesial end flat, thin, and squarish.	Much as in the Bush-Tits.	Resembles <i>Psaltiriparus plumbeus</i> .	Quite as we find it in the U. S. Bush-Tits.	Iliia meet the sacral crista. The double row of pits present.	This little Timmouse from the N. W. Himalayas, osteologically comes near our genus <i>Psaltiriparus</i> , and in some particulars especially in the skull, nearer <i>Chamaea</i> .





being related to the *Miminæ*, in that subfamily we find such a form as *Galeoscoptes carolinensis*, which not only lays greenish blue eggs, but also sometimes has the tarsal scutella obsolete (it being generally so in *Chamæa*). This and other minor points present themselves which will keep the fact before our minds that originally all these forms came from the same stock, and in the divergence which has subsequently taken place, in time, species have been created that are now remotely affined, as are such forms as *Galeoscoptes carolinensis* and *Chamæa fasciata*. Still Darwin has shown how such characters as I have mentioned above may be retained by the now more distantly related forms, and be transmitted by them.

So far then as the color of its eggs are concerned, it, as a character, points to the troglodytine affinity of *Chamæa*, probably in the way I have indicated, as birds directly related to the Wrens, as we have just seen, lay greenish blue eggs, and we are thus not compelled to pass beyond the limits of the family lines to obtain a likely explanation of this fact. At the present time I do not recall any typical parine form which lays an unspotted blue egg.

Recently I have had the opportunity of examining both *Campylorhynchus brunneicapillus* and *Auriparus flaviceps* in the flesh, several specimens of each. The former has all the characters of a large Wren, more nearly related to the species associated in the genus *Harporhynchus* than are any of our smaller Wrens; while the latter, notwithstanding its peculiar coloration, and some other non-strictly external parine characters, has a skeleton essentially very much like that part of the anatomy in *Psaltiriparus* and its allies.

Before recapitulating the skeletal characters for comparison, of a number of the species we have been examining in the present connection, I would again lay stress upon the fact that in so far as its topographical anatomy and characters are concerned, *Chamæa* shows a far closer kinship with *Psaltiriparus* than it does with any of our typical North American Wrens. In the matter of coloration simply, its predominating shades of brown seem to point Wren-wards; still we must remember here that in the case of the inland form of *Chamæa* (*C. f. henshawii*) the prevailing tints of the plumage are of a grayish ash, which Coues admits is "about the color of a *Lophophanes*."<sup>1</sup> Already

<sup>1</sup> *Key*, 2d ed., p. 262.

I have said, that when the species now grouped in the genus *Cinnicerthia* come to be anatomically examined and carefully compared, they may show quite as much of the Tit in their organization as they do of the Wren. Indeed, they may stand directly between these two groups of birds, and the new *Cinnicerthia* described by Mr. Sharpe in the Catalogue of the British Museum, may prove to have far more of the Wren in it than has *Cinnicerthia unibrunnea*; or still more than *C. unirufa*. Our hard and fast lines in systematic classification are a little binding sometimes, and do not strictly define the delicate relationships existing among such forms as go to make up the class *Aves*.

#### CONCLUSIONS.

It is only when one comes to investigate the morphology, in its entirety, of the smaller passerine birds, that it can in any way be appreciated how thickly the twigs stand upon that branch of the genealogical avian tree. As they have forked and split up, and been derived from each other, so have the bird forms which now represent this branching growth, become distinct in their thousand and one species, and in each we may look for inherited characters that likely they assumed and appropriated from a variety of ancestors at various stages of their derivation and off-shooting. Thus it is that we may come across a species of bird wherein the main trend of its morphology and organization is indubitably stamped with all the characters of the stock-branch, or that off-shoot where all those of its kind could be designated as clearly differentiated *Passeres* for instance, and yet it will show in *different degrees* tinctures in its make-up that have been borrowed by its economy from the earlier branchings that preceded it.

We may have a passerine bird presented to us, to offer an hypothetical case, which, to all intents and purposes, is in its entirety a representative of the great group which we have defined by that name. It may be the most *fixed* species of its genus, and yet when we come to study its structure in *all* its details, how puzzlingly do the anatomical evidences of its affinity crop up. So dilute may have some of the blood of remotely affined tribes run into itself that it lies quite beyond the power

of man to detect them, much less accurately state from whence they were derived. Then again, other characters present themselves which almost stand boldly out in their significance, and point but in one direction to the kindred stock responsible for them. Who is the one among us who can truly tell just *exactly* how much of *Steatornis* is Owl, or how much typical picine stock there is in *Yunx*? And such problems are even still harder to solve where the affines are thickly clustered, and such are the difficulties we meet with when one attempts to unravel the ancestry of such a species as *Chamæa fasciata*.

Apart from its larger size, there is no question, after we have stripped specimens of all our United States Wrens and Titmice of their feathers, but that the *general form* of a *Chamæa* is more like a Bush-Tit (*Psaltiriparus*) than it is like any of the rest of them, and this resemblance is real. Not to pass beyond the avifauna of this country then, we have shown in the text how this resemblance is again supported by the anatomy of the "soft parts,"—greater preponderance of characters of these birds being found in *Chamæa* over its troglydytine ones. Coming to the skeleton, a part of the organization from which we have the right to draw upon for our conclusions, it being one of the most reliable systems, and one which long retains the indices of a vertebrate's affinities, we see, at least, something to assist us in pronouncing upon the kinship of *Chamæa*.

Surely no one could be made to believe that *Chamæa* bears any close osteological resemblance to such a form as *Catherpes m. conspersus*. The short-faced, semi-rotund skull of the former, with its maxillo-palatines having their free mesial ends large, thin, flat, and *squarish*; with its palatines having *rounded* posterior-external angles, and with a differently formed vomer and mandible;—certainly all this is quite at variance with the long-faced, strikingly *flattened* skull of the latter, with its maxillo-palatines having their free mesial ends *narrow*, thin, and posteriorly produced; with its palatines having their postero-external angles produced and *angular*; and finally, with the differences in the vomer and mandible spoken of in the text of this monograph. These cranial differences, as we now know, are also supported by others in the trunk skeleton in the two species in question. Withdrawing, then, such a form as *Catherpes m. conspersus*, we find it followed by its evident allies in our



fauna, the representatives of the genera *Troglodytes*, *Salpinctes*, *Campylorhynchus*, and others, although many of these show, perhaps, a somewhat closer affinity with *Chamæa* than does *Catherpes*, but behind that fact it still remains clear that they are all WRENS in every sense of the word. *Campylorhynchus*, which by some has been supposed to be nearer *Chamæa*, has a typical Wren's skull, and one reminding us not very much of the Wren-Tit.

One of the best cranial characters distinguishing these birds is to be found in the form assumed by the free mesial extremities of the maxillo-palatines; these differences I have already clearly defined above, and they are *constant*; and furthermore, these parts are alike in *Chamæa* and *Psaltiriparus*, and differ from all the Wrens. The sternum offers us hardly a distinguishing character, but it would seem that the fact whether or no the ilia meet the sacral crista mesially should have its weight, and here *Campylorhynchus* is the only Wren that agrees with *Chamæa* in that particular, whereas the Bush-Tits practically add this feature to the other list of characters that force us to believe them to be more nearly related to *Chamæa* than any other species of bird at present known to our avifauna.

As I have already stated, judging from topographical anatomical characters alone, I am strongly inclined to think that *Chamæa fasciata* may be related to the *Cinnicerthia unirufa*, of Colombia, but I am also convinced that that latter species is not a whit nearer in its affinity to such a *Wren* as is *Catherpes m. conspersus*, than is *Chamæa*.

Whether *Cinnicerthia* has any parine affinity, and just how much, is a question, I believe, that still remains for the morphologist to decide.

## ERRATA AND ADDENDA

TO

VOLUME III., PART 2.



Page 142, line 21 from top; for "digits," read phalanges.

" 178, " 7 from bottom; for "chance," read change.

" 182, " 19 from top; for "commences," read commenced.

" 203, " 14 from top; insert after "water," the words, and air.

" 205, " 1st; for "these," read their.

" 208, " 10 from top; after "placed," add the words, over or.

" 208, " 15 from top; for "invertebrates," read vertebrates.

" 215, " 2 from top; for "metapophysis," read metapophyses.

" 217, " 5 from top; for "cause," read use.

" 240, " 14 from top; for "away," read way.

" 248, " at bottom of page; insert, after Gaudry.

" 261, last line of explanation of Fig. 83; for "external," read intermediate.

" 266, last line of explanation of Fig. 87; for "tympania," read tympanic.

" 268, first line of explanation of Fig. 90; for "(a)," read (c).

" 273, line 7; before "assertion," insert the word naked.

" 277, " 13 from top; for "transverse," read longitudinal.

















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